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Soybean seed yield, viability and vigor, and chemical composition resulting from drought and high temperature stress during seed fill

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Soybean seed yield, viability and vigor, and chemical composition resulting from drought and high temperature stress during seed fill

by

David L. Dornbos, Jr.

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INTRODUCTION

The primary goals of seedsmen are high yield and good seed quality which are determined by genotype, environment, and their interaction. The soybean plant frequently is exposed to drought and/or high temperature stress of varying intensity and duration during the growing season. Energy budget relationships can be used to describe the dynamic exchange of energy between a leaf and its environment. Stress intensity can be quantified by application of energy budget relationships to measured values of leaf and air temperature. Energy budget methods can also be used to estimate leaf temperature, transpiration, and photosynthetic rates. Models utilizing energy budget relationships are capable of predicting such parameters for a variety of environmental conditions.

Drought stress, particularly that which occurred during pod formation and seed fill, linearly decreased soybean seed yield, because the yield components seed number, seed mass, and seed number per pod were reduced. Air temperatures above 30 C also caused yield reductions.

In contrast to yield, little is known about the effect of environmental stress on the viability, vigor, and chemical composition of the soybean seed. While it is generally recognized that seed quality is reduced by environmental stress that also reduces yield, quantitative

data relating seed quality and stress are unavailable.

Although the vigor tests of seed quality have been correlated with field emergence, the physiological mechanism(s) responsible for vigor loss because of environmental stress are unknown. One proposed mechanism of seed quality loss suggests that loss of membrane integrity is a first step in the deterioration process. The conductivity test, a test of seed vigor, represents a measure of seed membrane integrity. Membranes of low quality seed leak greater quantities of electrically conductive solutes than does high quality seed. Membrane lipid composition is determined in part by the environmental growth conditions, and determines the fluidity, and therefore integrity, of a membrane when exposed to a particular set of environmental conditions. The phospholipid composition associated with fluid membranes in the seed fill environment may cause membranes to be nonfluid and leaky, indicating reduced vigor, in the germination environment.

In addition to the effect of drought and high temperature on yield, viability, and vigor, chemical composition of the seed may be altered. Studies have reported that air temperature induced change in the oil content, and fatty acid composition of the seed, but did not influence the protein content. The effect of drought

was unknown. Therefore, the economically important chemical components of grain that might be altered by environmental stress during seed fill, affecting the utilization properties of the grain.

Because air temperature, humidity, and other factors are vertically-stratified within a plant canopy, the vertical position the pod assumes on the plant may affect pod temperature. Pod temperature may affect characteristics such as yield, viability, vigor, and chemical composition.

A research project was undertaken to consider the following objectives:

1) To impose three levels of drought at several air temperatures on soybean plants during seed fill and to quantify the intensity of stress using a remotely-measured plant parameter.

2) To quantify the effect of stress on leaflet productivity, seed yield and the yield components, and viability and vigor of seed from several plant positions.

3) To characterize the energy budget relationships of soybean leaflets exposed to drought and high temperature stresses.

4) To measure the effect of drought and high temperature on protein and oil content, and fatty acid composition.

LITERATURE REVIEW

The harvest of large yields of vigorous seeds is a goal of high priority to most soybean (Glycine max [L.] Merr.) seed producers. Economic success or failure hinges upon attaining satisfactory yields in most years. To the producer's dismay, environmental conditions are seldom optimum throughout a growing season, resulting in reduced quantity and quality of grain produced. Two environmental extremes of frequent concern are drought and high temperature. High air temperatures and poor water-holding capacity of southern and tropical soils often hinder successful soybean production. In the western U.S. plains, where seasonal evaporation can exceed rainfall by two- to three-fold, successful soybean production is not possible without irrigation. Even in the Midwest, where the soybean is equally suited with corn (Zea mays L.) to summer temperature and rainfall patterns, intermittent environmental stress is typical. Environmental stress can reduce yield from 0 to 70%, depending upon the intensity of stress, its duration, and the time during the developmental process when it occurs. Nearly three-quarters of the variability of soybean yield in the Midwest can be attributed to non-optimum environmental conditions (Runge and Odell, 1960). Environmental stress reduces photosynthetic rates, and therefore yield potential. Yield

reductions are primarily the result of the production of fewer and smaller seeds. Seed of reduced viability and vigor, and altered chemical composition, are also produced as a consequence of stress, affecting utilization of seed and grain. Because air temperature (AT) is vertically stratified in the crop canopy, the nodal position at which a pod develops could affect these seed characteristics. To facilitate comparison of stress effects between years and locations, and the development of predictive computer models, it is essential to quantify stress intensity. Air and canopy temperature differences can potentially be used to measure stress intensity. The role of stress in altering growth and seed quality parameters is of primary importance and basic to the understanding and implementation of sound management practices under different environmental regimes in soybean production areas throughout the world.

Leaflet Productivity

While the relationship between the carbon dioxide fixation rate and yield are incompletely understood, it is clear that yield is coupled with photosynthetic rates. When adequate photoperiodic photon flux density and soil moisture were available, Jeffers and Shibles (1969) found canopy photosynthesis of three soybean cultivars exhibited

an optimum rate of 60 mg CO_2 m^{-2} s^{-1} between 25 and 30 C.

The stomatal conductance and net photosynthesis of potted soybeans were reduced by drought (Sionit et al., 1984). Bennett and Albrecht (1984) found leaf water potential decreased within 12 days after water was with held from vegetative pot-grown soybeans. Apparent photosynthesis and nitrogen fixation decreased concomitantly with leaf water potential, and stomatal resistance increased. Cortes and Sinclair (1986) found drought resistance of 'SRF150' soybeans was conferred because the plant maintained a high leaf water potential through the development of a large root system and a low resistance to internal water transport.

The canopy temperature of drought-stressed alfalfa (Medicago sativa L.) plants was 8.5 C warmer than control plants at mid-day than control plants (Carter and Sheaffer, 1983). The difference in canopy temperature resulted from stomatal closure when the intensity of solar radiation was high. As soil moisture became progressively deficient, stomatal resistance and leaf temperature increased while transpiration and apparent photosynthetic rates decreased.

Yield and the Yield Components

To assure profitability, attainment of maximum yield is the primary objective of most producers. Under optimum

conditions, soybean yields can reach 4.3 Mg ha^{-1}. Runge and Odell (1960) found drought and high AT accounted for 68% of the soybean yield variation between 1909 and 1957.

The effects of high AT and drought on yield and the yield components are well known. The reduction in vegetative growth and yield was determined by the duration, severity, and stage of development during which drought occurred. Indeterminate 'Evans' soybeans grown in the field produced yields of 400, 2,400, and 3,290 kg ha^{-1} when 0, 203, and 277 mm of water were delivered during the growing season (Cox and Jolliff, 1986). The non-irrigated treatment reduced field-grown determinate 'Braxton' soybean yield from 3,068 to 1,400 kg ha^{-1} (Wallace, 1986).

The yield reduction was greatest when drought occurred during pod formation or seed fill. Sionit and Kramer (1977) found that drought during soybean reproductive growth reduced the yield of both cultivars studied. Meckel et al. (1984) measured a 20 to 50% reduction in vegetative plant size and a 21 to 46% reduction in yield when severe drought was imposed at R5. Earlier stresses did not affect yield. Ramseur et al. (1984b) found irrigation throughout the season or only at bloom increased yield by 55% relative to the non-irrigated control, from 2,950 to 1,322 kg ha^{-1}, respectively.

Yield is also variable because of drought that occurred

during different stages of reproductive development. Irrigation during pod and seed development increased yield by 379 and 384 kg ha^{-1}, respectively, relative to non-irrigated controls (Korte et al., 1983a). Kadhem et al. (1985a) irrigated soybean plants at 10 d intervals between R1 and R6. Single irrigations at R3.7 or R4.7 gave maximum yields because the period from mid-pod elongation to seed enlargement was most responsive to irrigation for deteminate and indeterminate cultivars.

Soybean yield was reduced by day/night AT greater than 30/25 C (Egli and Wardlaw, 1980). Seddigh and Jolliff (1984) found that a night AT of 16 C gave a maximum soybean yield of 25.5 g seed $plant^{-1}$, but a night AT of 24 C at the same daytime AT reduced yield 8%.

The seed yield of each soybean plant can be partitioned into the components: pod number, seed mass, and seed number per pod. Yield was more highly correlated with seed number than with seed mass (Egli, 1975; Egli et al., 1978; Gbipki and Crookston, 1981; Ramseur et al., 1984a). Korte et al. (1983b) and Wallace (1986) reported a close relationship between pod and seed number, and yield. Seed mass was not correlated with yield (Ramseur et al., 1984a). Spaeth and Sinclair (1984) found mean mass per seed was negatively correlated with seed number. The variation in individual seed mass within a cultivar could not be

explained by plant position, seed fill rate or duration.

Seed mass is determined by the seed fill rate and duration (Egli et al., 1978). Numerous investigators have shown that yield is more closely related to seed fill duration than rate (Egli and Leggett, 1973; Egli et al., 1978; Dunphy et al., 1979; Gbipki and Crookston, 1981), although variation in the seed fill rate did contribute to yield (Egli and Leggett, 1973; Kaplan and Koller, 1974). Egli et al. (1984) found significant differences between genotypes for reproductive duration. The effective filling period (EFP), calculated by dividing the mass of the mature seed by the daily rate of mass accumulation during seed fill, of 59 soybean genotypes varied between 29 and 57 days. Similarly, the number of days that elapsed between R5 and R7 varied between 42 and 55 days. They concluded that genotypes with long filling periods could be useful for developing higher yielding soybean cultivars, even though genotype x year interactions occurred frequently. Beaver and Cooper (1982) measured seed fill rates of 13.6 and 11.3 g m^{-2} d^{-1} for Maturity Group II 'Corsoy' and Maturity Group III 'Williams' soybeans, respectively, but seed fill duration was shorter for 'Corsoy'. The greater seed fill rate of 'Corsoy' was attributed to a larger number of seeds per unit area rather than faster accumulation per seed. Egli et al. (1978) found that seed

fill rate varied from 3.6 to 8.0 mg seed^{-1} d^{-1} among several soybean cultivars.

Effects of environmental stress on yield can be explained by considering the yield components. Pandey et al. (1984a) found that the linear yield reduction of several grain legumes because of decreased water supply could be explained, in order, by decreased pod number per plant, seed number per pod, and individual seed mass. Heindl and Brun (1984) found that differences in yield between 1981 and 1982 resulted from variable flower and pod abscission rates, and therefore reduced seed number. Seed number per pod was constant at 2.3.

The cause for the yield increase because of irrigation can also be explained by considering the yield components. Wallace (1986) found that irrigation increased yield by increasing the number of harvestable pods. Seed number per pod, seed mass, the EFP, and seed growth rate were unaffected by irrigation. Korte et al. (1983b) reported that irrigation between R3 and R4 increased seed number and yield, but seed mass remained constant. Irrigation between R5 and R6 increased seed mass and yield, but seed number remained constant. Irrigation treatments that did not affect yield resulted from off-setting increases in seed number and decreases in seed mass (Korte et al., 1983b). Irrigation throughout the growing season or once at bloom

gave a similar yield increase (Ramseur et al., 1984a). Seed number was increased similarly by both irrigation treatments but seed mass was unchanged. Kadhem et al. (1985b) measured a positive correlation with seed mass and irrigation from R4.7 to R6.4 when seed number was fixed, but not from R1.1 to R3.7 when seed number increased with irrigation. Greater potential existed for irrigation to increase seed number than mass, particularly with indeterminate cultivars (Kadhem et al., 1985b).

Yield and the yield components were affected by high AT. Egli and Wardlaw (1980) found that seed growth rate and seed fill duration were relatively insensitive to day/night AT of 24/19 C to 30/25 C during seed fill. AT above 30/25 C increased the seed fill rate but decreased duration because of rapid leaf senescence. The EFP was reduced three days when the plants were exposed to day/night AT of 33/28 C in the growth chamber, resulting in reduced seed mass (Egli and Wardlaw, 1980). High AT during flowering and pod set decreased the seed growth rate and yield, suggesting that seed growth rate was partly determined by environmental conditions during early development. Studies with seeds grown on plants and cultured _in vitro_ suggested that AT reduced the seed growth rate directly in addition to limiting photosynthate supply (Egli and Wardlaw, 1980). Ketring (1984) found that peanut (_Arachis hypogaea_ L.)

yield was reduced by the day/night AT regime of 35/22 C because fewer subterranean pegs and smaller seeds were produced. The effect of high AT is not entirely separable from the drought effect, because high AT can indirectly impose a high heat-load. Variability for tolerance to high AT did exist among peanut genotypes (Ketring, 1984). Seed number and mass can be reduced by environmental stress during seed fill.

The yield components are not uniformly distributed within the soybean canopy. Ramseur et al. (1984b) found 'Braxton' pod number and yield were maximum, but seed number per pod and seed mass were minimum, from the lower half of canopy nodes. Pods and seeds from entire branches were included with the node from which the branch originated, potentially confounding the effect of vertical stratification. Wallace (1986) divided 'Braxton' soybeans into lower, middle, and upper strata and found that smaller seeds and fewer seeds per pod were associated with lower strata. The upper canopy stratum was most responsive to irrigation. The proportion of yield from the upper stratum increased from 33 to 42% of the total because more pods were produced (Wallace, 1986).

Individual seed mass can be reduced by stress. Egli et al. (1987) found that the average individual seed mass of a seed lot was reduced by source-sink manipulations, planting

date, and varied among cultivars, because the distribution of individual seed mass varied within each seed lot. The range of individual seed mass within a seed lot did not change. Seed lots produced in unstressed environments contain large and small seeds, but stressed environments caused a greater proportion of small seeds to be produced, reducing the average mass per seed.

Seed Viability and Vigor

Good soybean seed viability and vigor is important to seedsmen, because seed lots that contain a large proportion of viable and vigorous seeds are demanded by producers for planting. Germination is defined as the emergence and development of those essential structures from the seed embryo that are needed to produce a normal plant under favorable conditions (AOSA, 1986). The standard germination test, described in the Rules for Testing Seeds (AOSA, 1986), is the most widely accepted test for estimating seed viability.

Unfortunately, viability tests are inadequate predictors of field emergence for two reasons: 1) seldom are field conditions optimum as assumed by standard test conditions, and 2) seedlings are classified as either germinable or non-germinable after a seven-day period without regard to the progressive nature of seed deterioration (McDonald,

1980). Predictive accuracy of the standard germination test ranged from 0 to 41.7% (TeKrony and Egli, 1977). The highest accuracy was obtained when field conditions were nearly ideal. Standardization and evaluation of additional seed tests are needed to accurately, reproducibly, and objectively predict field emergence (McDonald, 1980).

The concept of seed vigor was developed to complement viability. Vigor is defined in the Vigor Testing Handbook (AOSA, 1983) as those seed properties that determine the potential for rapid, uniform emergence and development of normal seedlings under a wide range of field conditions. Accepted vigor tests include: 1) the accelerated aging test to evaluate seed storability, 2) the cold test to evaluate emergence ability in cool, wet, unsterilized soils, 3) the conductivity test to estimate seed membrane integrity, 4) the cool germination test to estimate germination ability in a cool microorganism-free environment, 5) the relative growth rate test to evaluate the ability to convert seed storage reserves into seedling axis dry weight, 6) the seedling vigor classification test to allow partitioning of germinated seedlings into strong and weak categories, 7) and the tetrazolium test to identify living seed tissues.

TeKrony and Egli (1977) found that the range in vigor test values was wider than for the standard germination

test values, indicating an improved ability to distinguish quality differences among seed lots. Seed vigor results were more closely related to field emergence under stress conditions than standard germination test results (Egli and TeKrony, 1979).

Several researchers developed an index by combining viability and vigor test results to accurately predict field emergence across a wide range of field conditions. DeLouche (1974) suggested that a vigor index should include the standard germination test and a combination of vigor tests. Johnson and Wax (1978) correlated accelerated aging results with field emergence in 1975, but not in 1976. The cold test was correlated with emergence both years. Johnson and Wax (1978) stated that it seemed impossible for a single test, or group of tests, to be capable of predicting field emergence reliably for all the conditions to which a seed could be exposed. TeKrony and Egli (1977) measured a field emergence prediction accuracy of 63.9% for soybean when the results of standard germination, 4-day germination, and accelerated aging germination tests were combined into a single vigor index, but only 38.9% when individual test results were compared. Yaklich and Kulik (1979) combined the results of standard germination, seedling vigor classification, seedling length, and tetrazolium staining tests and measured a predictive

accuracy of 50 to 60%.

No minimum seed-quality level that prevents yield loss has been established. By branching profusely, soybeans can compensate for stand reductions of up to 30% without a yield reduction. Johnson and Wax (1978) found that seed lots with extreme seed-quality differences had the same yield in unstressed environments. In stressful environments, however, vigor as determined by the cold test was correlated with yield. High vigor seeds increased yield indirectly by improving the plant population. Without a stand differential, high vigor seed conferred no yield advantage (Egli and TeKrony, 1979). Vigorous seed reduced the probability of a yield reduction in environmentally unfavorable years because a uniform stand of vigorous plants was established (AOSA, 1983).

A chronic problem facing the soybean seed industry is the production of seeds that possess low vigor (TeKrony et al., 1980). In many instances, the maximum seed quality level attainable is below minimum acceptable standards. It is not known how the environment affects seed physiology and biochemistry during development (TeKrony et al., 1980). Environmental stress can reduce seed quality (TeKrony, 1980). Soybean seed quality can be reduced by extremes in temperature, rainfall, and fungal infection (TeKrony et al., 1980).

While viability and vigor can be lost before or after physiological maturity (PM), when the seed possesses its maximum mass and quality, the environmental influence before PM has been studied less (TeKrony et al., 1980). Accumulated high AT during soybean seed development reduced germination percentage and seedling axis dry weight linearly (Keigley and Mullen, 1986). Seeds that developed under a day/night AT regime of 27/22 C in the growth chamber exhibited a standard germination percentage of 84%. Plants exposed to a high AT (32/28 C) for 35 and 60 days (until R8) produced seeds with germination percentages of 73 and 56%, respectively. DeLouche (1980) found that severe stress which interrupted seed development caused light, shriveled seed to be produced. TeKrony (1980) found that the environmental effect on seed quality was greater than the genetic effect, accounting for the variation among years.

Environmental stress between PM and harvest maturity (HM) can also reduce soybean seed quality. Green et al. (1965) reported that early-planted soybeans produced seed with lower standard germination and field emergence rates when maturation occurred during hot, dry weather. If maturation occurred either before or after a hot and dry period, higher-quality seed were produced. Low quality seed lots contained greater proportions of green cotyledons

and wrinkled seedcoats.

After HM, the seed is stored on the plant in the field until harvested. Seed quality can decline rapidly during this period. Four factors can affect soybean seed quality decline after HM: 1) alternate wetting and drying, 2) hot and dry conditions, 3) hot and wet conditions, and 4) a genetic effect (TeKrony et al., 1980). While genetic variability existed between 'Cutler 71' and 'Kent' at HM for seed quality, the rate of decline following HM was related to the field environment (TeKrony et al., 1980). Seed produced in various environments exhibit a broad range in viability and vigor. It is important, therefore, to determine how the environment can reduce seed quality.

No consistent relationship has been found between seed mass and viability or vigor (Edwards and Hartwig, 1971; Johnson and Leudders, 1974; Wetzel, 1975). Hoy and Gamble (1985, 1987) separated soybean seeds according to mass and density, then measured the speed and percentage of emergence. Seeds with large mass and low density from lots of intermediate vigor exhibited the poorest laboratory (Hoy and Gamble, 1985) and field (Hoy and Gamble, 1987) emergence, particularly in cool and wet, or crusted soils. Seeds with low mass were not the best performers regardless of density. Seed mass had no effect on yield, but high density seeds outyielded low density seeds in late

plantings (Hoy and Gamble, 1987). Crusting soils may affect emergence ability of seeds as a function of dimension. Seeds with large dimensions may also be damaged during mechanical harvest. Seed density can vary independently of seed mass and may be more directly related to viability and vigor.

Seeds that develop at different strata within a soybean canopy encounter different microclimatic and microbial conditions, and may affect viability and vigor. In addition, seeds develop during different periods of time at the same stratum because of differences in growth habit, and may be exposed to different environmental conditions. In a field study, Adam (1983) found that seeds from the upper half of indeterminate 'Amsoy 71' soybeans had higher standard and accelerated aging germination percentage, seedling growth rate, and mass. The higher quality of seeds from top positions may be due to lower disease pressure or different environmental conditions during seed development.

Chemical Composition

Soybean grain is valued commercially as a source of edible oil for human consumption and protein meal for animal feed. At maturity, soybean seeds are composed of approximately 42% protein (85% soluble), 23% oil, 9%

soluble carbohydrate, 5% pentosans, 5% crude fiber, and 16% hemicellulose (Bils and Howell, 1963). Protein and oil percentages are inversely related. Breeding efforts that increased protein content to 50% were accompanied by reduced oil content (Hartwig, personal communication. In Caldwell, 1973).

Dicot seed-storage proteins consist of the globulins vicilin and legumin (Bewley and Black, 1978), that are located in protein bodies at maturity (Graham and Gunning, 1970). Hill and Breidenbach (1974) separated three soybean protein classes with sedimentation coefficients of 2.2S, 7.5S, and 11.8S. The non-enzymatic storage proteins were homogeneous and consisted of repeated amino acid sequences. Major amino acids stored at maturity include: glutamate, aspartate, asparagine, and arginine (Catsimpoolas et al., 1967; Yazdi-Samadi et al., 1977).

Soybean oil is comprised of 95% neutral triglyceride (Norman, 1978). Fatty acid composition of mature 'Williams 79' soybean seed oil was 11.1, 4.2, 25.5, 53.2, and 6.0% of palmitate (16:0), stearate (18:0), oleate (18:1), linoleate (18:2), and linolenate (18:3), respectively (Dornbos and McDonald, 1986).

Soybean oil also contains phospholipid, representing 1.5 to 5.0% of the total, glycolipid, and tocopherol. Phospholipid classes contained in mature soybean seeds

include phosphatidylcholine, phosphatidylethanolamine, and phosphatidylinositol, representing 46.0, 25.0, and 17.4% of the total, respectively (Wilson and Rinne, 1974). Phospholipid is involved in triglyceride biosynthesis (Kennedy, 1961; Wilson et al., 1980; Wilson, 1981), and are membrane constituents (Goodwin and Mercer, 1983).

Seed composition varies with stage of development, environmental conditions during development, and pesticide exposure. Dornbos and McDonald (1986) described the time-course of fatty acid, carbohydrate, and protein composition change between R4 and R8.

Weiss et al. (1952) correlated the mean AT with oil content during pod and seed growth. Soybean seeds from plants exposed to daytime AT of 29.4, 25.0, and 21.1 C during seed fill contained 23.2, 20.8, and 19.5% oil, respectively (Howell and Cartter, 1958). The AT during 20 to 40 days before maturity, when the majority of oil accumulated, was most highly correlated with oil content (Howell and Cartter, 1958). Yield, acetone soluble oil, protein, and non-protein nitrogen were unaffected by AT during seed fill (Howell and Cartter, 1958).

AT affects sunflower (Helianthus annuus L.) seed oil content variably. Canvin (1965) measured maximum oil content at 21 C. Harris et al. (1978) found oil content decreased when AT increased. Unger and Thompson (1982)

found oil content decreased when AT decreased. Finally, Robertson et al. (1979) and Seiler (1983) found oil content was unaffected by AT. In addition to AT, Seiler (1983) related changes in oil content to daylength. Green (1986) found flax seed (Linum usitatissimum L.) oil content increased when AT increased from 15/10 to 30/25 C in a glasshouse. Higher AT reduced oil content and seed mass. AT affects the oil content of seeds from several crop species.

Fatty acid composition is affected by genotype and AT. Oleate and 18:2 content of sunflower oil is negatively correlated with AT, and 16:0 and 18:1 are positively correlated (Seiler, 1983). Linoleate and 18:3 content of flax oil decreases when AT increases because oleate desaturase activity is reduced by high AT (Green, 1986). Linolenate desaturase is unaffected by AT. In genetically improved low 18:3 flax lines, oleate desaturase activity and 18:3 content were unaffected by AT (Green, 1986).

Wilson et al. (1980) found that 18:2 and 18:3 are produced by the consecutive desaturation of 18:1. Altered unsaturated fatty acid composition is genetically regulated, at least in part, indicating potential in the selection for reduced 18:3 by use of recurrent selection (Wilson et al., 1981). By comparison of midparents, Wilson et al. (1981) estimated that polyunsaturated fatty acid

could be reduced by 54%. Selection for low 18:3 indicated that the genotype and environment interact (Cramer and Beversdorf, 1984). Carver et al. (1986) found that soybean lines with low 18:3 exhibited less environmental variability for 18:3 content than unselected lines. Minimum and maximum AT explained 84 and 69%, respectively, of the mean variability for 18:3 content. They suggested that AT may exert the greatest effect on fatty acid composition. The sensitivity of oleate desaturase activity to high AT in soybean is unknown. The effect of drought on fatty acid composition is unknown.

Nutrient deficiencies and pesticides also affect soybean seed composition. Wilson et al. (1982) found that oil percent decreased and protein increased when manganese became deficient. Palmitate, 18:0, 18:1, and 18:3 percentages increased, but 18:2 decreased. Penner and Meggitt (1970) treated two soybean cultivars with 13 herbicides and found that oil percentage was unaffected, but fatty acid composition was altered and yield reduced. Simazine (2-chloro-4,6-bisethylamino-s-triazine) treatment did not affect seed composition (Johnson and Jellum, 1969).

Plant position affected seed chemical composition. Collins and Cartter (1956) found that soybean seeds from the lower half of the plant contained 0.5% more oil and 1.0% less protein than those from the upper half. Seeds

from terminal pods of a raceme contained 2.0% less oil than seeds from basal pods. Terminal seeds within a pod contained slightly more oil than basal seeds from the same pod.

Stress Quantification

Numerous methods are available that enable quantification of the environmental stress intensity received by a plant. Methods vary in cost, accuracy, and difficulty. The stress degree day (SDD) index developed by Idso et al. (1977) utilized the Stefan-Boltzman Law, given in the following equation:

$R = e\ (s)\ T^4$, where,

R = long-wave radiant emittance of the source ($W\ m^{-2}$), e = emissivity of the source surface, and T = the objects temperature in degrees Kelvin, and s = the Stefan-Boltzman constant ($5.673 \times 10^{-8}\ W\ m^{-2}\ K^{-4}$). Using this equation, the temperature of an object can be calculated if R is known. An infrared thermometer determines the thermal energy (R) within the sensors field-of-view and calculates the objects temperature. Clawson and Blad (1982) found that corn plants, when irrigated on the basis of canopy temperature determined by infrared thermometry, used water more efficiently than control pots. No systematic effect of crop architecture was found with corn, nor was variation

in leaf temperature (LT) affected by AT (Clawson and Blad, 1982).

AT and soil moisture are environmental factors strongly coupled with crop yield. The intensity of stress received by a plant is difficult to determine using independent environmental factors because of variability in root volume, root activity, and disease. Idso et al. (1977) proposed the SDD index to non-destructively assess stress intensity using a plant characteristic:

SDD = alpha-beta (sum from i=b to e SDDi), where alpha and beta are constants, and SDDi is the difference between LT and AT in degrees Celcius at solar noon on day i, and b and e represented the days on which the summation was to begin and end, respectively. Yield was directly related to the accumulation of SDD during the reproductive phase with durum wheat (Triticum durum L.)(Idso et al., 1977). The intensity of stress imposed on corn was accurately assessed when the canopy temperature of stressed and well-watered plots were compared (Clawson and Blad, 1982). Harris et al. (1984) found that cumulative SDD was negatively and linearly related to soybean yield when evaporative demand was high.

Blad and Rosenberg (1976) found LTs of alfalfa foliage that were measured with an infrared (IR) thermometer or thermocouple (TC) differed by more than 1 to 2 C, except

during midafternoon, when agreement was within 0.5 C. Hatfield (1979) reported that individual Phaseolus LT measurements agreed closely with those of thermistors, TCs and IR thermometers. Canopy temperature measures differed most when canopy ground-cover varied from 20 to 50%, but the difference decreased as the ground-cover approached 100% (Hatfield, 1979). Kimes (1980) found that nadir temperature measurements of a wheat canopy using an IR thermometer did not differ from those measured with thermistors if the canopy was full, but agreement decreased as ground cover was reduced. Off-nadir measurements of canopy temperature minimized the problem but introduced differences due to variation in solar azimuth. Nielson et al. (1984) observed that a range of LTs could be measured depending on view direction and solar azimuth. They recommended using an average of the temperatures measured from several view directions to approximate true canopy temperature.

Soybean leaves and leaflets are capable of adjusting their orientation relative to the source of direct solar radiation to minimize the stress load (Shackel and Hall, 1979). When drought increased and leaf water potential decreased, terminal leaflets moved to a vertical position (Oosterhuis et al., 1985). At a critical leaf water potential of -1.4 MPa, the leaflets inverted. Oosterhuis

et al. (1985) found that upper canopy leaflet angle represented a visual indicator of drought. Changes in leaf angle due to drought reduced the quantity of light intercepted by the canopy (Turner, 1979), and reduced LT (Shackel and Hall, 1979).

LT may be greater or less than AT. Gardner et al. (1981) found that LT of stressed corn plants are often below AT. LT is strongly affected by the AT, relative humidity, and windspeed (Jackson, 1982). The crop water stress index (CWSI) was developed to account for the vapor pressure deficit, which is determined by AT and relative humidity (Jackson et al., 1981). When the vapor pressure deficit was large, as in dry environments, the CWSI index predicted canopy-air differences of 10 to 15 C (Jackson, 1982). In humid environments, the change in vapor pressure deficit did not fully reflect the change in AT so that CWSI did not accurately reflect stress intensity.

In addition to growth stage, the effect of a stress depends upon species. A CWSI of 0.3 may be the critical value for wheat but not cotton (Jackson, 1982). A critical CWSI may vary with stage of development for a particular species. Water stress prior to bloom in cotton may not reduce yield as much as a later stress (Guinn et al., 1981). In soybean, drought stress during vegetative growth decreased yield negligibly, but stress during flowering and

seed fill could potentially reduce yield a great deal (Meckel et al., 1984).

Conclusions

Drought and high AT reduces yield and the yield components. Because much of the soybean yield is derived from current photosynthesis, environmental stress that reduces photosynthetic rates would reduce yield proportionately as well. Yield is determined by the length of the reproductive period and the rate of seed fill, both of which are reduced by stress. Yield can be divided into the components of seed number, determined largely by pod number, seed mass, and seed number per pod. Each component is reduced by stress, but to differing degrees, depending on when stress occurs during reproductive development. Soybean seed viability and vigor is reduced by high AT. Accumulated stress causes linear declines in standard germination percentage and seedling axis dry weight. Oil content increases with AT, but protein content was unaffected. Linolenate content is reduced by high AT. The strata within the soybean canopy affected yield component response, viability and vigor, and seed chemical composition. No common method of stress measurement was used in the studies reviewed making quantitative comparison of stress effects difficult. Drought stress can be

nondestructively measured using infrared thermometry to measure LT. As drought increases, stomatal resistance increases, transpiration rates decrease and LT increases. Use of a plant characteristic to quantify stress facilitates the comparison, interpretation, and predictive modelling of stress effects.

PAPER 1. DROUGHT STRESS EFFECTS DURING SEED FILL ON SOYBEAN SEED VIABILITY AND VIGOR

Abstract

Little research has been devoted to the effect of the developmental environment on seed viability or vigor. The objective of this study was to relate the degree of drought stress that occurred during soybean (Glycine max (L.) Merr.) seed fill to reductions in seed viability and vigor. Drought stress was imposed on pot-grown plants in the greenhouse by applying differing volumes of water during seed fill. Drought stress intensity was measured by summing the daily difference between leaf and ambient air temperature to give the cumulative number of stress degree days (SDD). As SDD values increased from 46.2 to 141.2, indicating increased drought stress, leaf resistance increased 1.72 s cm^{-1}, transpiration decreased 79 mg H_2O m^{-2} s^{-1}, and apparent photosynthesis decreased 0.59 mg CO_2 m^{-2} s^{-1}, verifying that a severe drought stress had been imposed. Seed yield, viability, and vigor were reduced by drought. Seed yield was reduced linearly 38 and 59% in 1985 and 1986 primarily because fewer seeds were produced. Seed viability and vigor decreased linearly as SDD accumulated, but at different rates. Severe drought reduced standard germination percentage and seedling axis

dry weight 6 and 9%, respectively, and increased single-seed conductivity 14%. Seed quality loss was correlated with reduced single-seed mass. Severe drought that occurred throughout seed fill reduced yield and seed number to a greater extent than seed mass, viability, or vigor, thereby assuring the development of at least some viable and vigorous seeds.

Additional index words: Apparent Photosynthesis, Development, Germination, Glycine max (L.) Merr., Leaf Resistance.

Introduction

Large yields of viable and vigorous seeds are important goals for soybean seed producers. Seed yield, viability, and vigor can be reduced by environmental stress (TeKrony et al., 1980). Stress varies greatly in timing, intensity, and duration (Mederski et al., 1972). Understanding how stress affects yield and seed quality could facilitate the identification of useful traits for increased stress resistance.

Methodology has been developed for quantification of drought stress by comparing leaf biophysical parameters and air temperature (AT) using energy budget equations. Blad and Rosenberg (1976) found that elevated surface temperatures could be used to detect vegetation under

stress. Idso et al. (1977) introduced the stress degree day (SDD) index, defined as:

$$SDD = a\text{-}B \text{ (summation of } SDD_i),$$

where a and B represent constants and SDD_i is the midafternoon AT-leaf temperature (LT) difference summed over days i. They found that SDD was related to reduced durum wheat (Triticum durum L.) yield because of drought, possibly by detecting reduced photosynthetic rates. Similarly, soybean yield is negatively and linearly related to the number of SDD that accumulate during reproductive growth (Harris et al., 1984).

Drought stress during seed fill causes the largest soybean yield reductions (Meckel et al., 1984), primarily because fewer pods are produced, followed by fewer seeds per pod and smaller seed mass (Pandey et al., 1984). Irrigation after R4 increases yield, seed number, and in some cases, seed mass (Ramseur et al., 1984a).

Unfavorable environmental conditions during seed development and maturation can also reduce viability and vigor (TeKrony et al., 1980). DeLouche (1980) reported that stress severe enough to interrupt seed development resulted in light, shriveled seed. Soybean seeds that experienced hot, dry weather during maturation exhibited reduced laboratory germination and field emergence (Green et al., 1965). Little information is available concerning

the effect of environmental stress on the physiology of seed development and resultant seed quality (TeKrony et al., 1980).

Although environmental stress during seed development is known to reduce yield, the quantitative relationship between stress intensity, the yield components, and seed quality is unknown. The objective of this research was to relate the quantity of drought stress imposed during seed fill with reductions in seed viability and vigor.

Methods and Materials

On 15 Jan 1985 (Experiment I) and 18 Jan 1986 (Experiment II), seeds of the determinate soybean (Glycine max (L.) Merr.) cultivar 'Gnome' (Maturity Group II) were planted in 7.6-L plastic pots in equal parts of soil, peat, and perlite at the Agronomy greenhouse, Iowa State University, Ames, Iowa. Day/night AT of 20/16 C and 26/16 C were maintained throughout seed fill in 1985 and 1986. Fluorescent light banks were used to supplement natural sunlight 14 h per day in 1985, and high-intensity incandescent lights were used in 1986. Nitrogen, P, and K were applied at the rates of 2.4, 1.3, and 2.4 g per pot, respectively, in alternate irrigations during plant development.

In both experiments, 99 pots (two and one plants per pot

in 1985 and 1986, respectively) were arranged in a randomized complete block design with three replications. Within each replication three levels of drought stress were imposed, by use of a trickle irrigation system, when 80% of the plants had attained beginning seed fill (R5, Fehr and Caviness, 1977). The volume of water required to saturate control (well-watered) pots was delivered and measured each day, then 75 and 50% of that volume was delivered for moderate and severe drought-stress treatments.

To quantify drought stress intensity, an infrared thermometer (Everest Model 120), with emissivity of 0.98, was used to measure remotely the temperature of the uppermost fully-expanded leaflet that was normally exposed to direct solar radiation. Blad and Rosenberg (1976) and Hatfield (1979) found that LT measurement made with an infrared thermometer, thermocouple, or thermistor agreed within 0.2 C if only irradiated leaf tissue was within the sensors' field of view and measurements were made in midafternoon. LT was measured on sunny days near solar noon between R5 and R7 (physiological maturity). The infrared thermometer was held approximately 10 cm from the leaflet surface at a 30-degree angle. AT was measured simultaneously by use of laboratory thermometers shielded with aluminum foil within the canopy. The daily LT and AT

differences were used to calculate the number of SDD that accumulated between R5 and R7.

Apparent photosynthetic rate, transpiration rate, and leaf resistance of the tagged leaflets were measured on two dates during R6 (12 and 14 May 1986) by use of the LI-6000 Portable Photosynthesis System (LiCor, Lincoln, NE).

The reproductive period duration (RPD) was calculated for each plant as days between R5 and R7. Pods and seeds from each plant were hand-harvested, counted, and weighed after they reached R8 (harvest maturity), which is defined as seeds that dried to approximately 12% moisture. Seeds from the same replication, position, and drought-stress treatment were bulked, and stored in a cold room. Random samples were removed from these bulks, after mixing to disrupt stratification, for subsequent analyses.

Standard germination percentage was determined as described in the Rules for Testing Seeds (AOSA, 1986). Two vigor tests, relative seedling growth rate and single-seed conductivity, were used to measure seed vigor according to the Vigor Testing Handbook (AOSA, 1983). The seedling axis dry weight of normal seedlings from which the cotyledons had been removed was measured for the relative seedling growth rate test. The electrical conductivity of leachate from single seeds soaked in 1 ml of distilled water for 24 h was measured for the conductivity test.

Treatment effects were considered significant when P<=0.05, as determined by analyses of variance procedures.

Results and Discussion

As the volume of irrigation water applied to each plant during seed fill decreased, SDD values increased linearly and significantly both years (Fig. 1). The mean daytime AT during seed fill, measured within the shaded canopy, was 20 C in 1985 and 26 C in 1986.

To document the physiological effects of drought stress in this study, leaf resistance, transpiration and apparent photosynthetic rates were measured in 1986 (Table 1). As drought-stress intensity increased, leaf resistance increased 220%, and transpiration and apparent photosynthetic rates decreased by 45 and 69%, respectively. Drought intensity, when quantified by calculation of SDD, changed each physiological characteristic linearly. Correlation coefficients between SDD values and leaf resistance, transpiration and apparent photosynthetic rates were significant at 0.46, -0.57, and -0.68, respectively. Clearly, there was a relationship between these indices of plant function and drought-stress intensity, which was quantified by SDD. Sionit et al. (1984) also found that drought stress reduced stomatal conductance and net photosynthesis in leaves of field- and

pot-grown soybean plants.

Seed yield and the yield components were reduced significantly and linearly (regression data not shown) by drought stress during seed fill both years (Table 2). Across the entire stress intensity range, yield reductions were 38 and 59% in 1985 and 1986. The rate of yield loss because of drought was similar both years, as the slope of the linear regressions were -0.21 and -0.29 g seed SDD^{-1} for Experiments I and II. The greater loss of 1986 was reflected by the accumulation of a greater number of SDD rather than a greater yield loss per SDD. Pandey et al. (1984) and Meckel et al. (1984) measured similar soybean yield reductions of 20 to 50% due to decreased water availability.

Each yield component decreased significantly as drought stress increased, but at different rates (Table 2). Seed number was reduced 29% by severe drought in 1985 and by 52% in 1986. In contrast, seed mass decreased by 13 and 14% in 1985 and 1986. Because seed number per pod was unaffected by drought, the proportion of yield loss because of seed number and mass can be calculated using the percent change from control. Approximately three-quarters of the yield loss was due to fewer seed and the remainder to smaller seed. Pandey et al. (1984) found, with four indeterminate grain legumes, that drought affected the number of pods per

plant to the greatest extent, followed sequentially by seed number per pod and seed mass. Irrigation studies have also demonstrated that seed number was reduced to a greater extent than seed mass, particularly if irrigation water was applied late in the soybean seed fill period; seed number was changed through pod number rather than seed per pod (Ramseur et al., 1984a).

Seed mass, a primary component of yield, is determined by the rate of seed growth and duration of seed fill. In our study, seed fill duration was significantly and linearly reduced 16% by severe drought in 1985 and by 27% in 1986 (Table 2). Meckel et al. (1984) found the number of days that accumulated between R5 and R7 were reduced by drought stress and contributed to the yield reduction, and Egli et al. (1978) have shown there is a strong positive correlation between the duration of linear seed growth and final yield.

Unlike yield, quantitative effects of drought stress on seed viability and vigor, or physiological seed quality, have not previously been reported. As a result of severe drought, standard germination percentage decreased significantly and linearly by 6% when averaged across years (Fig. 2). Seedling axis dry weight decreased linearly by 10%, and seed conductivity increased linearly by 17%. Seed vigor tests, such as the relative growth rate and

conductivity, are thought to be more sensitive indicators of seed quality than are viability tests (McDonald, 1983). These data indicate that environmental stress during seed fill reduced vigor to a greater extent than viability.

Kadhem et al. (1985a) reported no effect of irrigation on visually observable seed quality. Visual estimates of seed quality are ineffective in separating low- and high-quality lots in many cases. Therefore, more powerful techniques are afforded by laboratory viability and vigor tests.

In 1985, seed mass and germination percentage, seedling axis dry weight, and single-seed conductivity were significantly correlated by 0.90, 0.95, and -0.79, respectively. In 1986, seedling axis dry weight and conductivity were significantly correlated by 0.85 and -0.95 with seed mass, respectively. Yield component changes implied that seed mass and quality are conserved to a large extent at the expense of pod and seed number in the event of severe drought. Therefore, the reproductive response of soybean to drought stress was to maintain seed mass, viability, and vigor at the expense of seed number, thereby maximizing the proportion of viable and vigorous seeds produced.

Conclusions

These results agree with Idso et al. (1977) that SDD relate drought to reduced yield by detecting reduced photosynthetic rates. Drought stress reduced seed number more rapidly than seed mass, thereby accounting for the linear yield reduction. Seed viability and vigor were linearly reduced as SDD accumulated, but at a slower rate than yield. The yield reduction because of severe drought was primarily due to the production of fewer seed, permitting the maintenance of seed mass and vigor. The relationship of yield, seed mass, viability, and vigor with SDD may be useful in the development of a predictive model.

Table 1. Transpiration, leaf resistance, and apparent photosynthetic rates of soybean plants exposed to three drought stress levels during seed fill

Drought Stress	Stress Degree Days	Transpiration Rate (mg H_2O m^{-2} s^{-1})	Leaf Resistance (s cm^{-1})	Photosynthetic Rate (mg CO_2 m^{-2} s^{-1})
Control	46.2	176.0	0.92	0.85
Moderate	110.8	114.1	2.21	0.38
Severe	141.2	97.0	2.64	0.26
SE	13.8	37.4	1.26	0.25

Table 2. Yield, seed number and mass, and reproductive period duration of soybean at three drought stress levels

Drought Stress	Stress Degree Days	Seed Yield (g plant^{-1})	Seed Number	Seed Mass (mg seed^{-1})	Reproductive Period Duration (d)
		1985			
Control	60.6	44.1	203	210	35
Moderate	91.7	32.4	154	193	34
Severe	140.0	27.3	147	182	29
SE	14.7	0.6	4	4	3
		1986			
Control	46.2	46.6	249	200	44
Moderate	110.8	35.6	195	197	38
Severe	141.2	19.2	121	172	33
SE	13.8	1.5	6	12	3

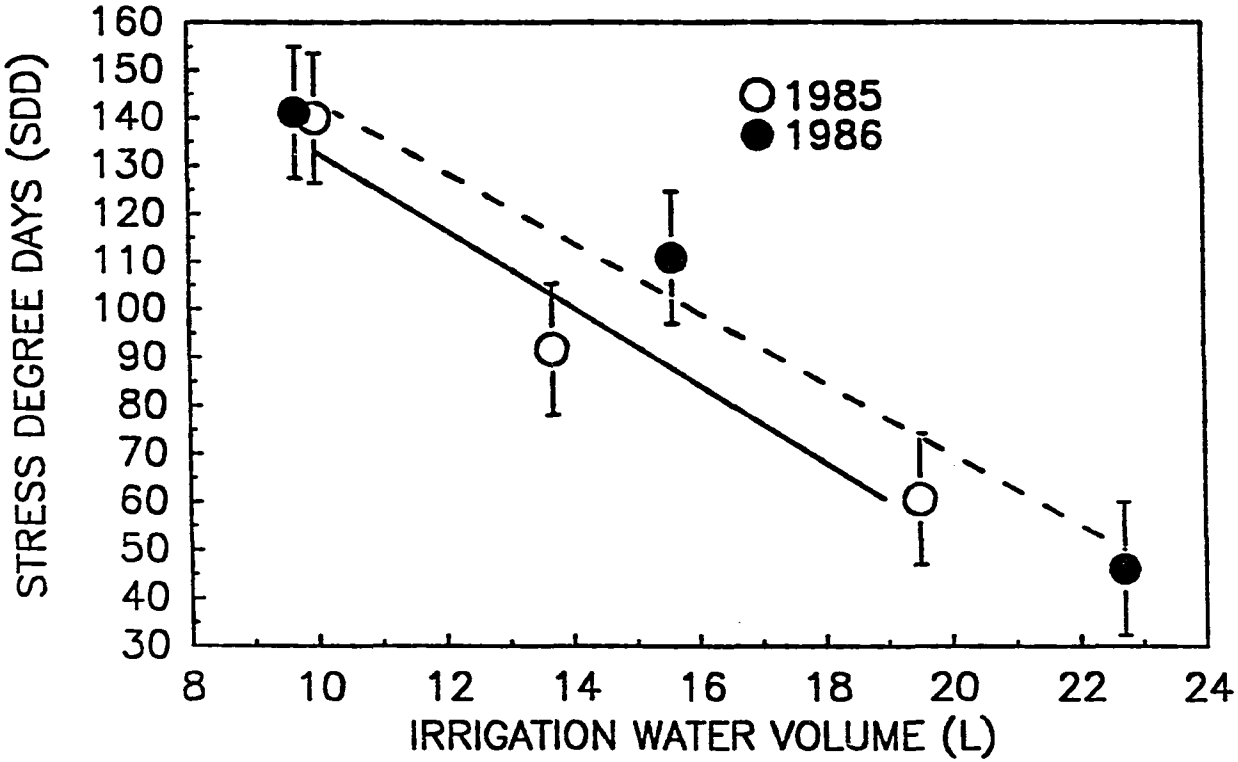


Figure 1. Stress degree day values of soybean plants exposed to three drought stress levels in 1985 and 1986

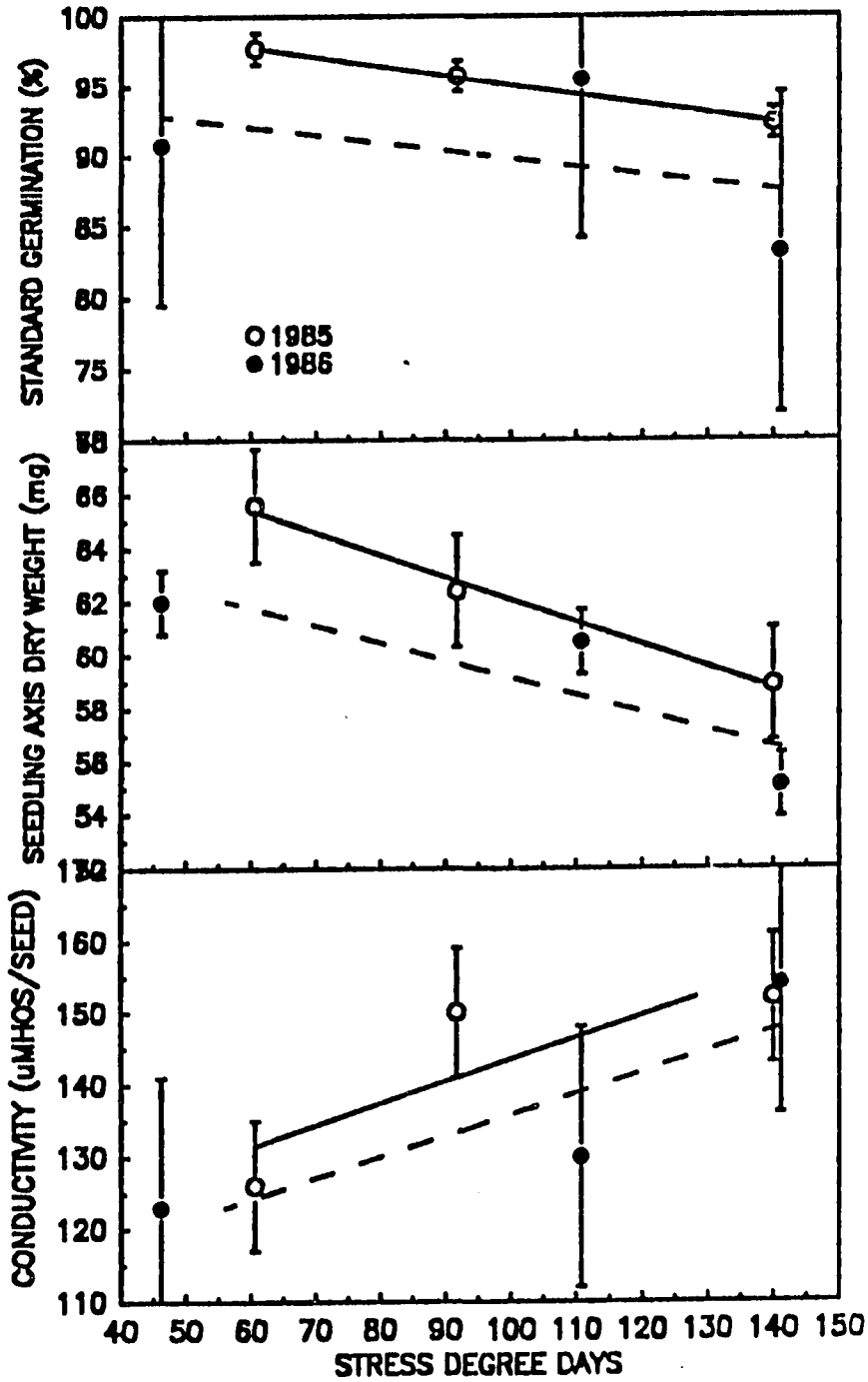


Figure 2. Standard germination, seedling axis dry weight, and conductivity of soybean seeds that were exposed to three levels of drought stress during seed fill in 1985 and 1986

PAPER 2. HIGH TEMPERATURE STRESS EFFECTS AT THREE DROUGHT STRESS LEVELS ON SOYBEAN SEED YIELD, VIABILITY, AND VIGOR

Abstract

Drought and high air temperature (AT) stress typically occur simultaneously during the growing season. The objective of this study was to determine the effect of an optimum and stressfully-high AT at three levels of drought stress on soybean (Glycine max (L.) Merr.) seed yield, viability, and vigor. Control, moderate, and severe drought levels were imposed on pot-grown indeterminate soybean plants in the greenhouse at daytime AT of 27, 29, 33, or 35 C by applying differing volumes of water during seed fill. Drought stress was measured by summing the daily difference between leaf and AT to give the number of stress degree days (SDD). With increased drought, SDD increased linearly from -21.7 to 40.8 at 34 C and from 32.3 to 84.4 at 28 C. Severe drought reduced yield from 36.1 to 21.0 g seed plant^{-1} at 28 C and from 26.9 to 12.9 g seed plant^{-1} at 34 C, because fewer and smaller seeds were produced. Seed mass was reduced 20% at 28 C and 47% at 34 C. Percentage germination and seedling axis dry weight (SADW) were reduced 3 and 17% by the stressfully-high AT. In addition, severe drought reduced the standard germination percentage and SADW linearly by 10 and 14%. AT

and SDD interacted synergistically in 1985 to reduce seed mass, viability, and vigor. Drought and high AT during seed fill reduced yield and seed quality independently and in synergistic interaction.

Introduction

Soybean yield, viability, and vigor can be reduced by environmental stress during seed development (TeKrony, 1980). The extent to which yield can be reduced by drought (Meckel et al., 1984) and high AT (Egli and Wardlaw, 1980; Seddigh and Jolliff, 1984) is well known. Little research has addressed the extent to which environmental stress is capable of reducing seed viability and vigor.

Soybean yield is reduced by daytime AT that exceed 30 C (Egli and Wardlaw, 1980). The seed fill rate and effective filling period are unaffected by day/night AT between 24/19 C and 30/25 C during seed fill, but they are reduced by an AT of 33/28 C (Egli and Wardlaw, 1980). Harris et al. (1984) demonstrated that soybean seed yield decreased linearly with increased drought during seed fill.

Cumulative high AT during seed fill linearly reduces germination percentage and seedling axis dry weight (SADW) of seeds from potted 'Century' soybean plants (Keigley and Mullen, 1986). Seeds that developed at the day/night AT of

27/22 C exhibited 84% germination, but those exposed to the high AT stress (32/28 C) for 35 and 60 d exhibited germination percentages of 73 and 56%, respectively. 'Gnome' soybean plants exposed to severe drought during seed fill produced seeds that exhibited a 6% reduction in germination percentage, a 10% reduction in SADW, and a 17% increase in conductivity (Paper 1, herein).

In many grain production areas, drought and high AT occur simultaneously. High AT may indirectly induce a plant water deficit even in the presence of adequate soil moisture because of internal resistance to water transport (Ketring, 1984). The objective of this study was to quantify the effect of a stressfully-high AT at three drought stress intensities on seed yield, the yield components, viability, and vigor.

Methods and Materials

During May of 1985 (Experiment I) and 1986 (Experiment II), soybean (Glycine max (L.) Merr.) seeds from the indeterminate Maturity Group I cultivar 'Hodgson 78' were planted in 144 7.6-L pots in the greenhouse in equal parts of soil, peat, and perlite. At V2, the plants were thinned to one per pot. The remaining plants were debranched at R3.

The experimental design was a split-plot randomized

complete block with AT and drought stress treatments representing the main and split-plots, respectively. At R5, 72 plants were placed in each of two similar adjacent greenhouse rooms with southern exposure. Daytime ambient AT was maintained 16 h per day at 29 C and 35 C in 1985, and 27 and 33 C in 1986. Night AT was 19 C in each room for both experiments. AT was measured continuously during seed fill using shielded hygrothermographs, one located in each greenhouse room.

The volume of water required to saturate the control pots in each room was delivered and measured each day, and 75 and 50% of that volume applied to impose moderate and severe drought-stress treatments, respectively. Drought stress intensity was quantified by measuring the stress degree days (SDD), the average daily leaf-AT difference summed during the seed fill period (Idso et al., 1977). After R7 (or physiological maturity), the plants were removed from stress until R8, which is harvest maturity.

At R8, pods and seeds were hand-harvested, counted and weighed. Seed lots receiving the same treatment were bulked and sufficient quantities randomly removed from each bulk, after mixing to disrupt stratification, for measurement of seed viability and vigor. Viability was measured using the standard germination rolled-towel test according to the Rules for Testing Seeds (AOSA, 1986), and

vigor was measured using the relative growth rate test as described in the Vigor Testing Handbook (AOSA, 1983).

Results and Discussion

In both experiments, SDD values increased at both the optimum and stressfully-high ATs as less irrigation water was delivered indicating increased drought stress (Fig. 1). Smaller SDD values were associated with the stressfully-high AT in contrast to expectation; because, as AT increased, a greater proportion of the heat-load imposed on a leaflet was alleviated by conductive, convective, and evaporative (a lower relative humidity was associated with the high AT) cooling. SDD values associated with the optimum or stressfully-high ATs at the same drought stress level were similar both years. The water volume applied to each plant was correlated across years with SDD values by -0.71 across AT and by -0.94 at 28 C and -0.93 at 34 C. SDD were more closely correlated with water supply when compared within an AT suggesting that AT affected absolute SDD values in addition to drought. A similar relationship occurred in 1985. The linear interaction between SDD and AT in 1985 indicated that SDD values increased more rapidly at the stressfully-high AT.

High AT reduced yield 37 and 22% in 1985 and 1986, respectively (Table 1). Yield was correlated with AT, r= -

0.47 in 1985 and -0.38 in 1986. Egli and Wardlaw (1980) found that a day/night AT of 33/28 C during pod fill reduced seed growth rate, duration, and yield. Results with seeds cultured in vitro suggested that AT directly affects seed growth. Seed yield of 'Hodgson 78' decreased linearly 59% in 1985 and 40% in 1986 because of severe drought (Table 1). Across AT, the slope of the regression lines were similar, -0.29 in 1985 and -0.23 in 1986, indicating similar rates of yield loss as a function of SDD and the absence of an interaction between drought and high AT for yield. Harris et al. (1984) also found soybean yield decreased linearly as SDD accumulated.

Drought and high AT reduced seed number and mass. The increase in AT from 29 to 35 C reduced seed number and mass 20 and 25% in 1985 (Table 1). Similar changes occurred in 1986. Severe drought linearly reduced seed number and mass 33 and 34% in 1985, and 27 and 19% in 1986. Seed number per pod was significantly reduced by severe drought only in 1986, and was unaffected by high AT. Irrigation during seed fill (between R4.7 and R6.4) increased seed number to a small extent but greatly increased seed mass, whereas earlier irrigation greatly increased seed number without affecting mass (Kadhem et al., 1985b). The linear reductions in seed number and mass by drought at optimum and stressfully-high AT accounted for

nearly the entire yield reduction.

The SDD x AT interaction for seed number was insignificant either year, indicating that severe drought reduced seed number at similar rates for both AT. A linear SDD x AT interaction occurred for seed mass in 1985, but not in 1986. In 1985, seed mass was reduced 21% by severe drought at 29 C, and 47% at 35 C. A negatively synergistic interaction occurred between drought and high AT for seed mass in 1985.

The reproductive period duration (RPD), the number of days between R5 and R7, was reduced 18% by 35 C in 1985 ($Pr<F$ 0.10) and 12% by 33 C in 1986 ($Pr<F$ 0.01, Table 1). The RPD was also reduced 29% by severe drought both years, as reported for several other cultivars (Korte et al., 1983a). A negative synergistic linear SDD x AT interaction occurred for RPD in 1985, but not 1986, and was correlated with seed mass ($r= 0.94$). In 1985, high AT reduced the RPD of control and severely drought-stressed plants by 6 and 32%. While seed fill rate did vary significantly between soybean cultivars, Egli et al. (1978) found yield was more closely related to the duration of seed fill.

High AT increased the proportion of hardseed, but drought had a small effect. High AT increased the proportion of hardseed from 1.9% to 8.6% in 1985, and from

23.6% to 55.2% in 1986 (Fig. 2). Although AT exhibited the greatest effect, drought also increased the proportion of hardseed, from 3.5 to 5.8% across AT in 1985, and from 26.7 to 56.0% in 1986. AT and SDD were correlated with percentage hardseed by 0.87 and -0.27. Hill et al. (1986) imposed successive 3-day wilt-recovery drought stress intervals and found the percentage of impermeable seeds from stressed plants increased as seed mass decreased (r= -0.92). In this study, seed mass was also correlated with percent hardseed by -0.71 in 1985 and -0.94 in 1986.

As with yield, seed viability and vigor were reduced by high AT and drought during seed fill (Fig. 3). Because high AT increased the hardseed percentage, all seeds were hand-scarified prior to conducting the standard germination and SADW tests, and the conductivity test could not be conducted.

Germination percentage was reduced 13.6 and 5.7% in 1985 and 1986 because of severe drought (Fig. 2). In addition, germination percentage decreased 2.9% when AT increased from 29 to 35 C across drought levels in 1985, and did not change in 1986 (Fig. 2). A 6% reduction in the standard germination percentage of 'Gnome' soybeans occurred because of severe drought during seed fill (Paper 1, herein). A linear (Pr<F 0.10) SDD x AT interaction occurred for reduced germination percentage in 1985, but not in 1986.

Germination percentage decreased 1.1% because of severe drought at 29 C, but by 26.0% at 35 C in 1985 (Fig. 2). Keigley and Mullen (1986) found germination percentage of seeds that developed at an AT of 32/28 C (day/night) was 58% lower than those that developed at 27/22 C. In addition to the high daytime AT, the elevated night AT of Keigley and Mullen (1986) may have contributed to the large seed quality reduction when compared with this study. TeKrony (1980) found that environmental stress during seed fill contributed to seed viability and vigor loss because of field weathering.

Seed vigor, measured using the relative growth rate test, was reduced by environmental stress during seed fill. SADW decreased 19% because of high AT in 1985, and 15% in 1986 (Fig. 2). As with germination percentage, high AT reduced SADW by up to 62% (Keigley and Mullen, 1986), substantially more than reported in this paper. SADW was also reduced linearly 15% by severe drought in 1985, but was unaffected in 1986. A negative, synergistic interaction between drought and high AT was significant and linear for SADW in 1985, but not in 1986. SADW of seeds from control plants was reduced 11% by high AT in 1985, but SADW of seeds from severely drought-stressed plants was reduced 31%.

Environmental stress that occurred during soybean seed

fill reduced seed viability and vigor. Ketring (1984) reported that drought and high AT stress effects were inseparable, at least in part, on a physiological basis (Ketring, 1984). Effects attributed solely to high AT may be due in part to the direct, negative effect of a stressfully high AT, but also in part to the indirect effect of a high-AT induced drought stress. The statistical interaction likely accounts for a portion of the physiological interaction, but not necessarily all of it. The physiological interaction between stresses may have contributed to the difference in magnitude of germination percentage and SADW reduction from high AT reported in this study and by Keigley and Mullen (1986). Because of resistance to water movement in the plant vascular system, drought stress may have resulted from the elevated AT in the growth chamber, even though adequate pot-moisture was available. Possibly, additional plant stress occurred from transferring potted plants grown in the field to the growth chamber at R5, where stress was imposed (Keigley and Mullen, 1986). Constant and elevated night-time AT reduced yield and the yield components of indeterminate field-grown soybeans (Seddigh and Jolliff, 1984), and may also have been a factor in the large seed quality reduction measured by Kiegley and Mullen (1986).

Seed mass, when reduced by environmental stress, was

correlated with viability and vigor. Seed mass and standard germination percentage were correlated by 0.89 in 1985, but not in 1986. SADW was correlated with seed mass by 0.87 and 0.92 in 1985 and 1986, respectively. It remains unclear if viability and vigor losses are a direct reflection of seed mass reduction, or a direct effect of stress being indirectly related to seed mass. The effect of seed mass or density on germination ability in the laboratory or emergence ability in the field is unclear. Several researchers have significantly related seed mass and quality, whereas others have found no relationship.

Conclusions

Reductions in seed viability and vigor by environmental stress were buffered by seed number. Seed number was reduced by severe drought at the optimum temperature to a greater extent than seed mass, accounting for the yield reduction, and seed viability and vigor were maintained. When severe drought occurred at the stressfully-high AT, both seed number and mass reductions caused a larger yield reduction, and viability and vigor were also reduced in proportion with the seed mass loss. The variable response of viability and vigor to environmental stress reported in past experiments may be at least partly due to differences in the plant buffering capacity of the seed number.

Table 1. Yield, seed number, seed mass, and the reproductive period duration of soybean plants exposed to three drought stress levels at 28 and 34 C two years

Air Temperature (C)	Stress Degree Days	Yield (g plant^{-1})	Seed Number (plant^{-1})	Seed Mass (mg seed^{-1})	RPD[a] (d)
			1985		
29	25.7	34.3	166	208	39
	40.5	24.0	132	192	36
	69.6	18.3	112	164	32
35	-19.3	24.4	131	188	37
	15.2	14.8	108	135	29
	47.0	8.7	87	99	22
SE[b]		1.8	8	12	2
SE[c]		2.3	6	28	5

[a]Reproductive period duration.

[b]Comparison of drought stress means within temperature.

[c]Comparison of temperature means within drought stress.

Table 1. continued

Air Temperature (C)	Stress Degree Days	Yield (g plant^{-1})	Seed Number (plant^{-1})	Seed Mass (mg seed^{-1})	RPD (d)
			1986		
27	38.8	38.0	204	188	35
	69.5	31.4	183	172	30
	99.2	23.7	148	159	29
33	-24.0	29.4	190	154	31
	4.2	26.4	174	150	28
	34.6	17.0	140	120	22
SE		1.7	11	8	1
SE		2.1	2	13	1

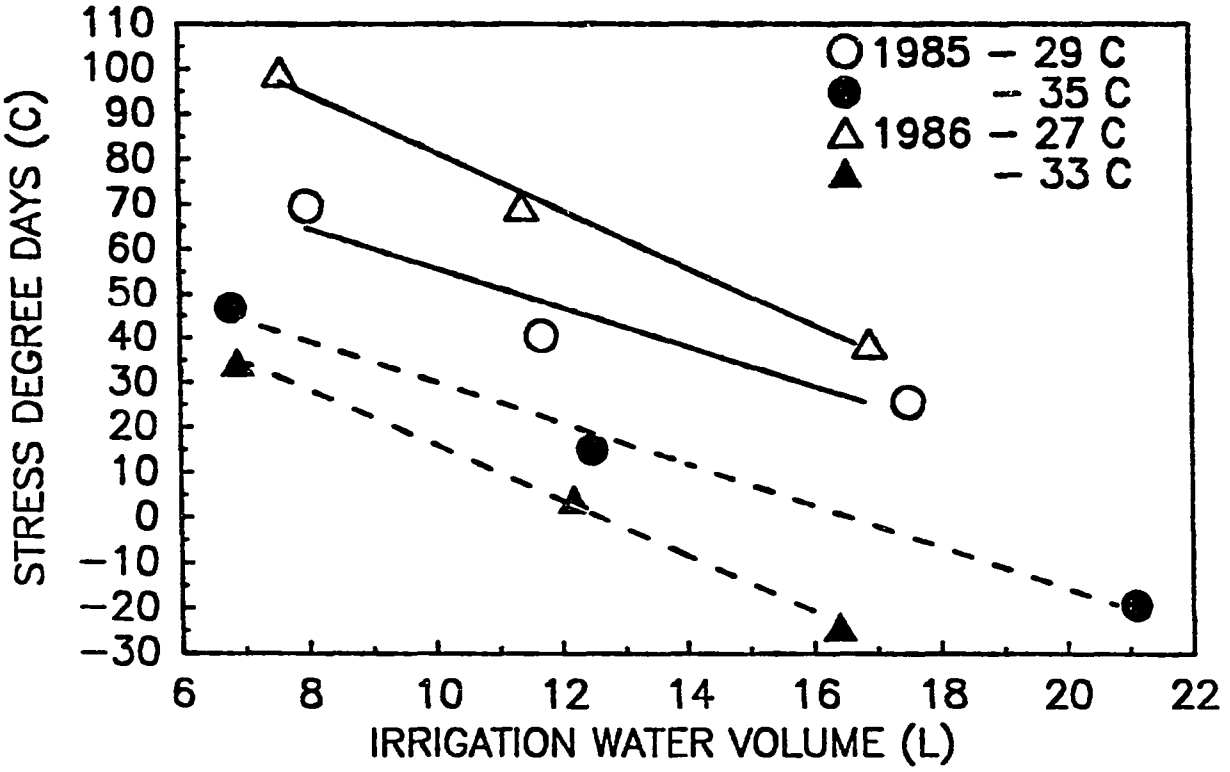


Figure 1. Stress degree day values of soybean plants exposed to three drought stress levels in 1985 and 1986

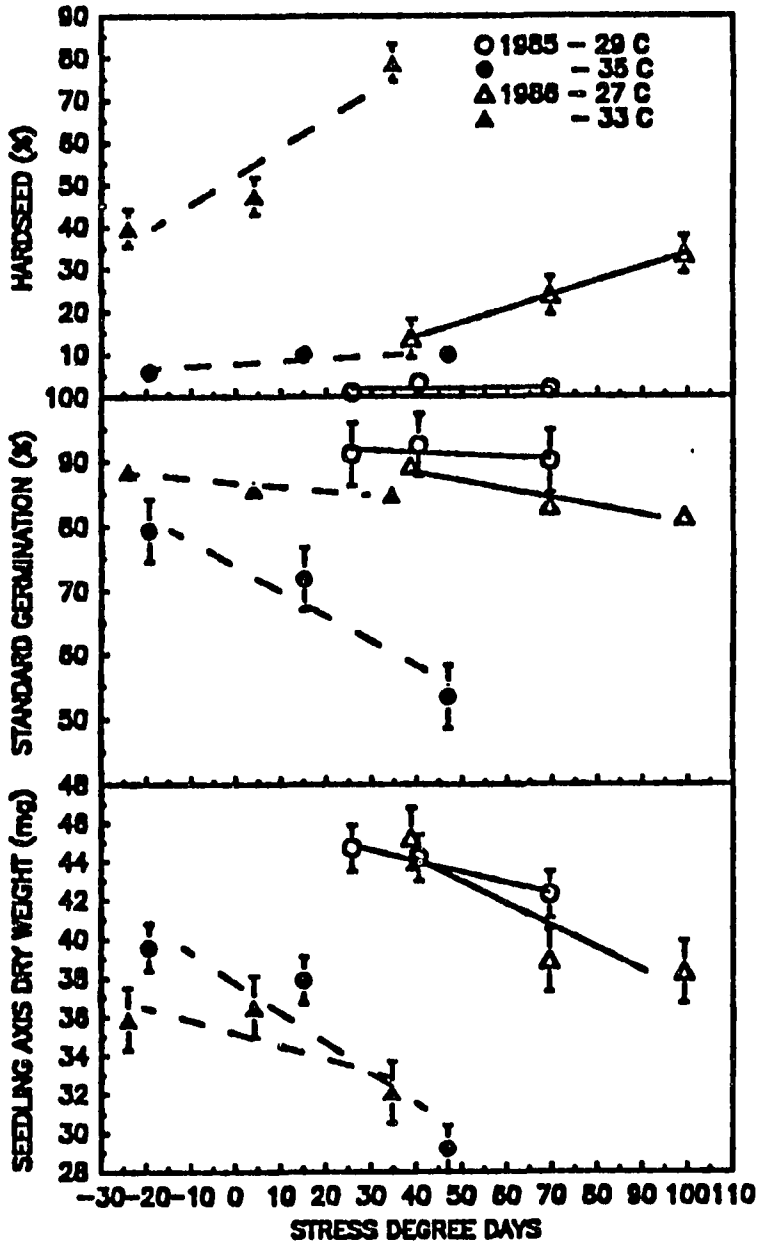


Figure 2. Percent hardseed, standard germination percent, and seedling axis dry weight of 'Hodgson 78' soybean seeds that were exposed to three levels of drought at an optimum and stressfully-high air temperature

PAPER 3. ENERGY BUDGET RELATIONSHIPS OF SOYBEANS GROWN IN STRESSED ENVIRONMENTS

Introduction

Environmental stress, particularly drought and high air temperature (AT), occur commonly and reduce crop productivity and yield. The quantity of stress received by a plant is dependent on numerous parameters such as leaf size and shape, AT, vapor pressure deficit, availability of soil moisture, and the internal resistance to water transport from the root to the evaporative surface. A complex integration of these components is necessary to quantify the stress received by a plant in a given environment. The direct measurement of a plant characteristic that responds to and integrates each of the independent parameters of the environment most accurately reflects the intensity of stress received by a plant.

Most stress quantification methods currently used require destructive sampling, expensive or cumbersome instrumentation, and are time-consuming. Leaf or canopy temperature (LT), however, can be measured rapidly and nondestructively with portable and inexpensive infrared thermometers.

To facilitate the development of models capable of

predicting the effects of stress in diverse environments, stress intensity must be quantified. Idso et al. (1977) developed the stress degree day (SDD) index to relate LT-AT differences to yield. Increased LT, relative to AT, suggests that the vapor pressure deficit to which the plant was exposed exceeded the plants ability to supply adequate water for evaporative cooling. Durum wheat (Triticum durum L.)(Idso et al., 1977) and soybean (Glycine max L.)(Harris et al., 1984) yield decreased linearly as SDD accumulated during seed fill. Because much assimilate for yield is derived from current photosynthesis, and photosynthetic rates are reduced by drought, Idso et al. (1977) theorized that the SDD index is negatively correlated with yield through a direct relationship with the photosynthetic rate.

Because the plant characteristic LT integrates the independent factors of the environment to which it is exposed, it can be used to assess drought stress intensity. Leaf energy budget equations utilize biophysical relationships to describe the dynamic exchange of energy between a leaf and the environment. The energy budget equations are applicable to a variety of environments and plants because they integrate the major independent factors that determine LT. Hence, LT provides a useful basis for the development of computer models relating stress

intensity to a variety of plant responses.

The objectives of this study were to: First, utilize energy budget relationships to predict LT for a broad range of leaf resistance and AT combinations; Second, compare predicted LT and SDD values with empirically measured LT, leaf resistance, transpiration and photosynthesis, and the SDD of plants exposed to three levels of drought at a wide range of AT.

Theoretical Model

Leaf temperature, the transpiration rate (E), leaf resistance (r), and photosynthesis (P) are interrelated, dependent plant processes. The independent environmental factors of air temperature (AT), vapor pressure deficit (vpd), relative humidity (h), and wind velocity (V), leaf dimension (D) and width (W), and the quantity of radiant energy absorbed (Qabs) are strongly coupled with the dependent plant processes. Quantitative knowledge of the independent factors are required to permit an understanding of the dynamic energy exhange between a leaf and its environment. Specifically, LT and E can be estimated for various environmental conditions using the equations given by Gates (1980).

Soybean plants were grown in pots in the greenhouse as part of four experiments (Papers 1 and 2, herein). Several

independent environmental factors were measured or estimated in association with these greenhouse environments. These variables were used to calculate theoretical LT values. The following independent factors were defined as constant and were used to calculate the predicted LT values:

1. Wind velocity (V) = 1.0 m s^{-1}
2. Absorbed radiation (Qabs) was estimated as follows:
   a) measured soil temperature = 24.3 C
   b) sky (glass) temperature = 24.3 C (measured using an infrared thermometer with emissivity (e) equal to 0.95)
   c) leaf absorptivity to solar radiation = 50%
   d) daily solar radiation (S_o) at noon, June 21, 42 N, was 1.2 cal cm^{-2} m^{-1} (Smithsonian Tables), or 837.2 W m^{-2}. Soybean seed fill occurred between mid-May and mid-August. While incident solar radiation in the greenhouse varied during this period reaching a maximum on June 21 differences during this time of year are minimal. For simplicity, variation in S_o was assumed to be zero.

Qabs = solar + sky + soil + reflected

$= [(\text{absorptivity})(S_o) + (e)(s)(T_{glass})^4 +$

$(e)(s)(T_{soil})^4 + (0.10)(S_o)]$/leaf plane = 727.4 W m^{-2}

3. Soybean leaf D and W:

   a) average maximum leaflet width = 0.09 m

      R_D = 0.699 (Taylor, 1974)

      D = 0.699 x 0.09 = 0.063 m

   b) average maximum leaflet length = 0.127 m

      r_W = 0.575 (Taylor, 1974)

      W = 0.575 x 0.127 = 0.073 m

4. boundary layer resistance (r_a)

   $=k_2[(W^{0.20})(D^{0.35})/V^{0.55}]$ = 45 s m^{-1}

The following equation from Gates (1980) was used to calculate predicted LT and E iteratively:

$$Qabs = (e)(s)(LT+273.14)^4 + k_1(V^{0.5}/D^{0.5})(LT-AT) + (l)(LT)[{}_sd(LT)-h{}^sd_a(AT)]/(r_s + r_a)$$

Constants used for this equation follow:

1) soybean leaf emissivity (e) = 0.98
2) Stefan-Boltzman constant (s) = 5.673 x 10^{-8} W m^{-2} K^{-4}
3) constant k_1 = 9.14 J m^{-2} $s^{-0.5}$ C^{-1}
4) latent heat of evaporation (l) of water at 30 C (the average daily LT) was 2.430 x 10^6 J kg^{-1}
5) ${}_sd(LT)$ and ${}_sd_a(AT)$ = water vapor density (kg m^{-3}) at LT and AT, respectively,

Calculated dependent values vary with changes in D, W, V, or h. Little variability existed for these parameters (data not shown), because h and V are controlled in the greenhouse and only the fully-expanded terminal leaflets of the apical leaves of two cultivars were used. Therefore, average measured values of h, V, D, and W were used. Qabs, AT, E, and r can vary widely, so a broad range of each of these parameters was used for LT calculation to bracket the environmental variability in the greenhouse.

Predicted LT

Predicted LT increased as a function of AT, r, and Qabs (Fig. 1). LT increased linearly with AT at each r. The rate of LT increase relative to AT was similar for each r-value. LT also increased proportionately as Qabs increased. A dashed line equating LT and AT is plotted on each figure. The area above the line represents LT warmer than AT. As AT increased, and as r and Qabs decreased, predicted LT occupied an increasingly larger area in which LT was cooler than AT, even though LT increased with AT. LT increased at a slower rate than AT because an increasingly larger proportion of the heat-load imposed on the leaf is lost by convection, conduction, and evaporation, and therefore is not reflected in the AT

values. Because increased Qabs that may accompany increased AT were not expressed for simplicity, it cannot be concluded that increased AT will always result in a smaller difference between LT and AT. The possibility of LT being less than AT has been long disputed. Jackson (1982) demonstrated that LT can exist below AT as a result of transpirational cooling, particularly when the vpd is large, as in arid environments.

The predicted transpiration rate of leaves increased as predicted LT increased for each Qabs and r combination (Fig. 2). Assuming a constant h, the vpd is primarily a function of Qabs. The transpiration rate at 50 s m^{-1} represents the volume of water that is required to maintain an optimum LT. As the vpd increased, the volume of transpiration water lost increased indicating the greater need for evaporative cooling. When leaf r increased, limiting the extent to which evaporative cooling could occur, LT increased relative to AT.

When the AT was high and r was low, evaporative cooling reduced the LT below AT (Fig. 1). As the level of Qabs and AT increased, the E rate increased when r was small, maintaining a given LT. E increased linearly for the same r, but at a faster rate at low r-values, resulting in a higher LT when the AT (and vpd) increased. If soil moisture is limiting then r, and therefore LT, increase as

a smaller proportion of evaporative cooling can occur. Increased r can reduce the photosynthetic rate both directly by limiting the rate at which CO_2 enters the leaf and indirectly by increasing LT. Therefore, LT and SDD provide a link between drought and the immediate photosynthesis rate, and subsequent yield.

Empirical LT, r, E, and P

Three drought stresses were imposed on potted soybean plants grown in a greenhouse at AT between 20 and 35 C. Stress was imposed between R5 and R7 because the largest reductions in soybean yield resulted from drought that occurred during seed fill (Sionit and Kramer, 1977). Stress was imposed by measuring the volume of water required to saturate the control pots, then delivering 75 and 50% of that volume to moderate and severely drought-stressed pots each day, respectively. AT of 20 and 26 C in Spring, 1986 and 1986, and 29 and 35 C in Summer, 1985, and 27 and 33 C in Summer, 1986, respectively, were controlled by thermostat adjustment in adjacent greenhouse rooms.

LT was measured remotely using an Everest Model 120 infrared thermomter. The temperature of one uppermost fully-expanded leaflet that was normally oriented to and illuminated by direct solar radiation was measured at solar noon. The thermometer sensor was held 5 to 8 cm from each

leaflet at a thirty degree angle from the plane of the leaflet, thereby ensuring that the sensor viewed only leaf tissue. Shielded hygrothermographs were used to measure the AT in each room.

LT increased with AT and increased drought (Fig. 3). LT increased linearly as a function of AT, but at a slower rate than AT. A 5.4 C increase in LT corresponded to a 11.2 C increase in AT. The rate of LT increase with increasing AT was similar for each drought stress level. LT increased by 2.4 and 1.7 C above unstressed controls because of moderate and severe drought, respectively. The LT difference associated with drought was similar for each AT.

As predicted by energy budget relationships, higher LTs, relative to AT, were associated with increased r, and decreased E and P (Table 1). Because of reduced soil water availability to the plant roots, insufficient water was capable of being supplied to meet the vpd. Leaf resistance increased 220%, attenuating the rate of water loss 45%. Two consequences concomitant with increased r were a 5.0 C increase in LT and a 69% decrease in the apparent photosynthetic rate. As predicted, a direct link existed between r, LT, and P. A stress of sufficient severity and duration would presumably cause yield to be reduced proportionately. Idso et al. (1977) found durum wheat

(Triticum durum) yield decreased linearly as SDD, the daily LT-AT difference, accumulated during seed fill. They theorized that the SDD index was indirectly related to yield because of direct relationship with the photosynthetic rate. Both the predicted and empirical data reported above support this conclusion.

A Comparison Between Predicted and Empirical LT

The trends of LT change relative to AT because of increased r and drought stress were similar whether predicted or empirically measured. To facilitate the development of predictive computer models of environmental stress effects, it is necessary to compare the magnitude of LT change in response to independent environmental factors. While LT represents an accurate evaluation of plant stress, because it is a plant characteristic, it remains necessary to understand the mechanism of LT change that resulted from the independent environmental factors.

In the greenhouse study of Spring 1986, the Qabs was estimated to be 727 W m^{-2}. Using the Qabs value of 750 W m^{-2}, the predicted LT of Figure 1 were compared to those measured empirically (Fig. 4). Unstressed, moderate, and severely drought-stressed plants exhibited LTs that, for the respective AT, were closely associated with resistance-

values of 250, 500, and 1,000 s m^{-1}, respectively. The LT-AT difference of each drought treatment was consistently aligned with the same r-value. Therefore, the rate of LT increase, relative to AT, was the same for predicted and empirical data. These data concur in maintaining that the soil moisture deficit limited the ability of the leaf to maintain a low resistance, so that LT increased relative to AT. The predicted r at which the empirical LT were aligned (Fig. 4) were not the same as those empirically measured at an AT of 26 C (Table 1). Unstressed, moderate, and severely-drought stressed plants exhibited r-values 2.7-, 2.3-, and 3.8-fold lower than predicted. Therefore, absolute SDD values did not represent an accurate stress intensity measure. Modification of the methodology to calculate SDD, however, may permit the measurement of absolute stress quantification values that accurately reflect stress intensity across a wide range of AT.

The optimum temperature of leaflet productivity is approximately 30 C in soybean (Norman, 1978). The LT of unstressed soybean plants tended to approach 30 C at a wide variety of AT (Fig. 4). With adequately watered soybean plants, LT was 4 C warmer than AT at 26 C, equal to AT at approximately 30 C, and 2 C cooler than AT at 33 C. At each AT, LT deviated toward the optimum LT for productivity suggesting that leaves were able to optimize

LT over a wide range of AT when adequate moisture was available. Viewed in another way, the environment that the soybean adapted to may have favored a LT of 30 C.

Stress Quantification Method

The SDD index developed by Idso et al. (1977) represents a potentially useful method for quantifying stress intensity. The number of SDD that accumulated during soybean seed fill in the previous two studies were calculated and plotted against the volume of water applied to each plant (Papers 1 and 2, herein). As soil moisture became limiting, the SDD values increased linearly at each AT, accurately indicating increased drought within an AT. As AT increased, however, SDD values decreased at each drought stress level, in contrast to what might be intuitively expected. Considering unstressed plants, 25.7 and -19.3 SDD accumulated at 29 and 35 C in 1985, respectively, and 38.8 and -24.0 SDD accumulated at 27 and 33 C in 1986. With severely drought-stressed plants, 69.6 and 99.2 SDD accumulated at 29 and 27 C in 1985 and 1986, respectively, but 47.0 and 34.6 SDD accumulated at 35 and 33 C. The stressfully-high AT reduced the yield of well-watered soybean plants by 37 and 22% in 1985 and 1986, respectively (Paper 2, herein), indicating that the high AT

did increase the stress intensity. Clearly, the absolute SDD values did not reflect the increased stress severity associated with increased AT.

Predicted LT increased more slowly than AT (Fig. 1), concurring with empirical data in indicating that predicted LT-AT differences decreased as AT increased. Increased AT contributes to the Qabs load imposed on a leaflet. The Qabs load is balanced by the reradiation of thermal energy, evaporative cooling, conduction, and convection, the proportions of which vary with AT. The proportion of the heat-load alleviated by reradiation, conductive, convective, and evaporative cooling is enhanced by increased AT. The greatest cooling effect is derived from evaporative cooling because a lower relative humidity, or dewpoint, and therefore vapor pressure deficit was associated with increased AT. Therefore, on the basis of the physical environment surrounding the leaf, LT and SDD increase more slowly than AT.

Energy budget equations can be used to modify empirically-measured LT and AT values to adjust SDD values for the AT effect (S. E. Taylor, Department of Agronomy, The Iowa State University, personal communication). The transient SDD equation is defined as follows: A sum during the seed fill period of the daily (i) value,

$$[(LT +/- x) - AT]i,$$

that was calculated for each sunny day that LT and AT was measured (Table 2). The value of x represents the temperature difference between the daily, empirically-measured AT and the predicted temperature of a leaf at a resistance of 100 s m^{-1} and a Qabs of 750 W m^{-1} (Fig. 1). Depending upon the AT, x can be positive or negative. A leaf resistance of 100 s m^{-1} was close to the value measured for unstressed (control) soybean leaves in the greenhouse (Table 1). LTs associated with leaf resistances above this baseline for a given AT infer stress. By quantitatively accounting for differences in AT and the r-values associated with initial stress, transient SDDs more accurately reflect stress intensity within and among a wide range of ATs.

The yield of 'Gnome' and 'Hodgson 78' soybeans were plotted against the number of transient SDDs that accumulated during seed fill in 1985 and 1986 (Fig. 5). Within an AT, yield decreased linearly when transient SDDs accumulated as before (Paper 1 and 2, herein). The number of transient SDDs that accumulated were similar for optimum and stressfully-high ATs. The effect of the stressfully-high AT in reducing yield was not reflected by a larger number of transient SDDs. Transient SDDs did represent an improvement, however, in that the number of transient SDDs associated with the high AT were not substantially lower

than those at the optimum AT, as seen before. It would be intuitively expected that more SDDs should accumulate when high AT is combined with severe drought than when severe drought occurs at an optimum AT. Transient SDD values better reflect drought and high AT stress than SDD values, but do not yet reflect absolute stress intensity.

An important independent environmental factor in addition to AT that strongly affects LT is h. Taken together, AT and h interact to determine the vpd. Jackson (1982) developed the crop water stress index (CWSI) by relating LT, AT, and h to account for the effects of both drought and AT. The vapor pressure deficit increases in proportion with increased AT. The rate of evaporative water loss from a leaf is determined by the vapor pressure deficit. Therefore, the CWSI incorporates the effect of AT on stress intensity to the extent that AT affects the vpd. AT is strongly coupled with the vpd when h is low, so that the CWSI represents an improvement on the SDD index by incorporating both drought and high temperature in a stress intensity measure. In humid environments, however, AT is weakly coupled with the vpd so that the vpd increase does not adequately reflect increased AT. CWSI did not represent an improvement upon SDD as a measure of stress intensity in the greenhouse environments (data not shown), presumably because h was too high, varying within the range

of 0.45 to 0.80.

Conclusions

Environmental stress during seed fill reduced soybean productivity and yield. Benefits emanating from the ability to quantify environmental stress using a non-destructive, rapidly-measured plant characteristic include the development of predictive computer models and irrigation management tools. Predicted LT, calculated using biophysical energy budget relationships, compared well with empirically-measured LT. The SDD method of quantifying drought stress intensity is limited because absolute SDD values were affected by AT. Because of the consistent manner by which AT affected the SDD index, however, potential exists for adjusting the method of calculating SDD to be able to compensate for AT. Energy budget relationships were used to predict the LT-AT difference of unstressed plants ($r = 100$ s m^{-1}) at the AT measurements were made each day. The LT-AT difference was used to modify the SDD equation for AT, giving a transient SDD equation. Absolute SDD values calculated using the transient SDD equations more accurately reflected drought stress intensity at a wide range of AT.

The energy budget model developed in this study, although proven to be realistic, was not applied in the

detail required to accurately describe all components of the field environments. In particular, attention was not given to variation of thermal background radiation in this study because the temperature of the glass "sky" was little affected by the AT. Sky temperature typically changes markedly with AT in the field. Incorporation of this and other factors into a model could provide an improved fit with empirical data, and therefore improved applicability to production environments.

Table 1. Terminal soybean leaflet and air temperature in relation to leaf resistance, transpiration, and apparent photosynthetic rate at three drought stress levels and an air temperature of 26 C

Drought Stress	Leaf Temperature (C)	Leaf Resistance ($s\ cm^{-1}$)	Transpiration Rate ($mg\ H_2O\ m^{-2}\ s^{-1}$)	Photosynthetic Rate ($mg\ CO_2\ m^{-2}s^{-1}$)
Control	27.7	0.92	176.0	0.85
Moderate	31.1	2.21	114.1	0.38
Severe	32.7	2.64	97.0	0.26
SE	0.7	1.26	37.4	0.25

Table 2. Air temperature, leaf temperature, and daily transient stress degree day (SDD) values for three drought stress levels

Air Temperature (C)	Leaf Temperature (C)			Transient SDD		
	C[a]	M[b]	S[c]	C	M	S
19.8	23.8	25.2	27.5	3.0	4.4	6.6
26.2	29.1	32.3	33.7	4.8	8.1	9.5
26.5	29.6	32.0	34.7	5.3	7.7	10.4
28.5	30.7	32.4	35.5	5.3	7.0	10.2
32.5	30.8	33.2	35.5	3.4	5.8	8.1
35.0	32.8	36.5	39.7	4.1	7.8	11.0

[a]Unstressed control.

[b]Moderate drought stress.

[c]Severe drought stress.

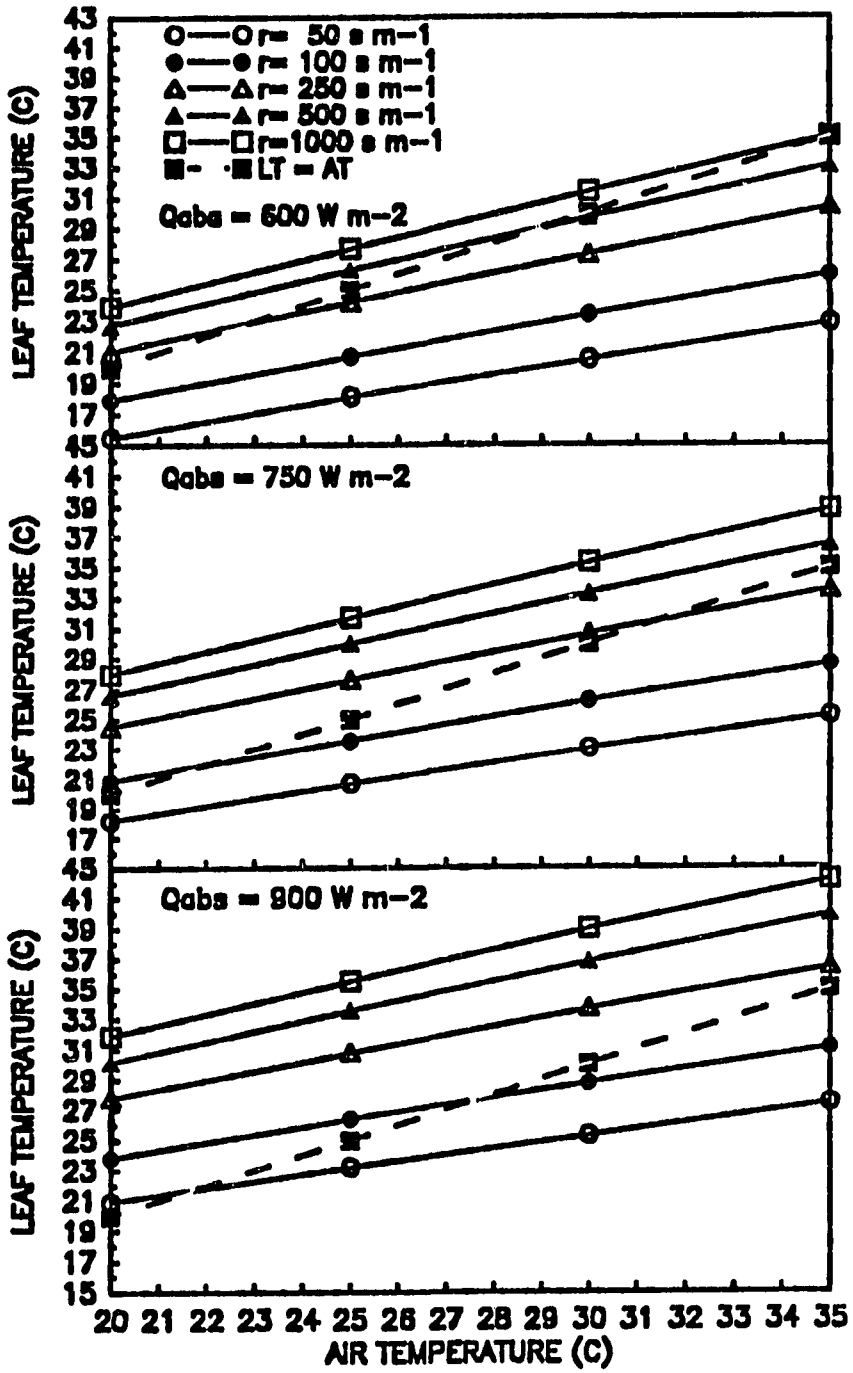


Figure 1. Leaf temperatures predicted using energy budget relationships for an air temperature range of 20 to 35 C and five leaf resistance levels

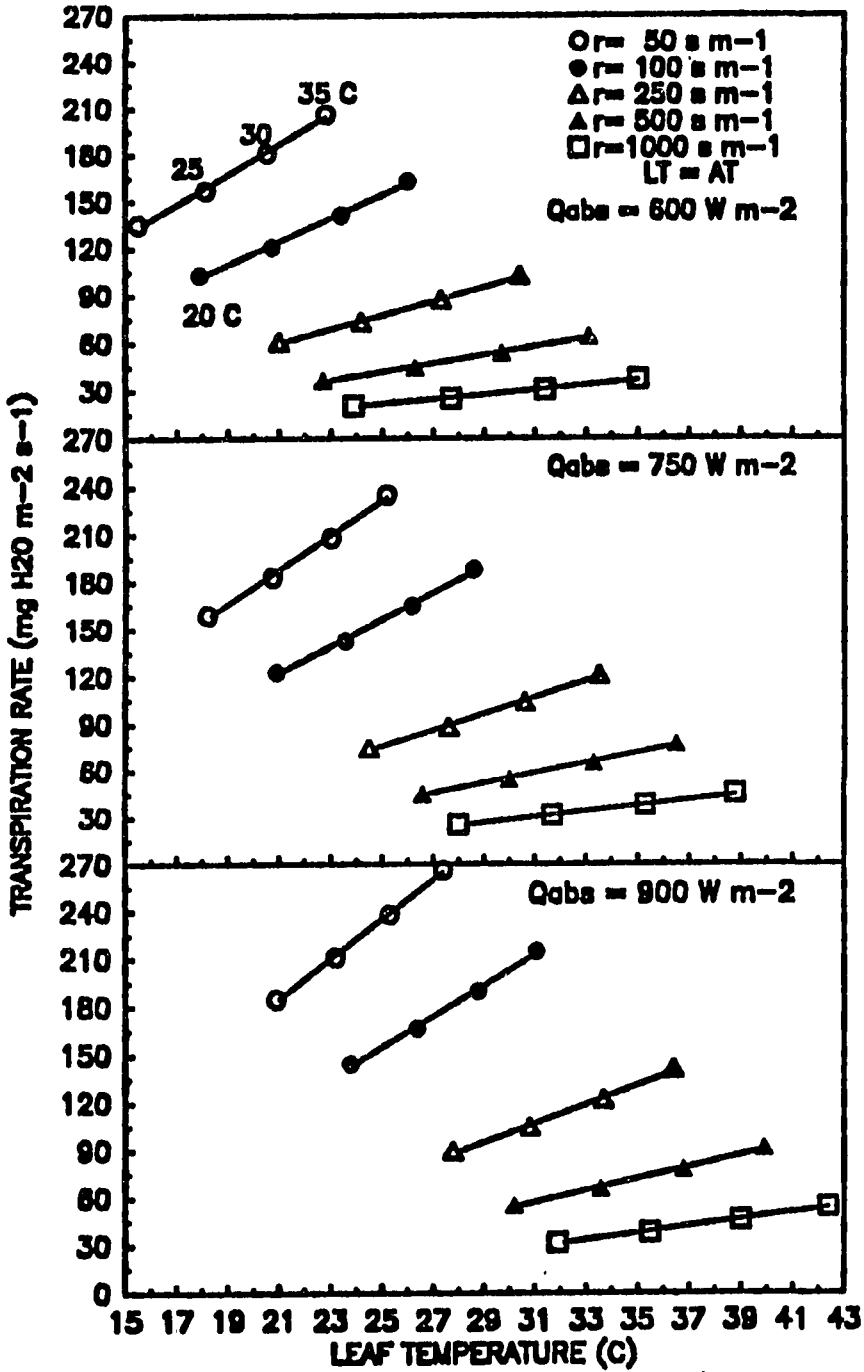


Figure 2. Transpiration rates predicted using energy budget relationships for an air temperature range of 20 to 35 C, a leaf temperature range of 15 to 43 C, and five leaf resistance levels

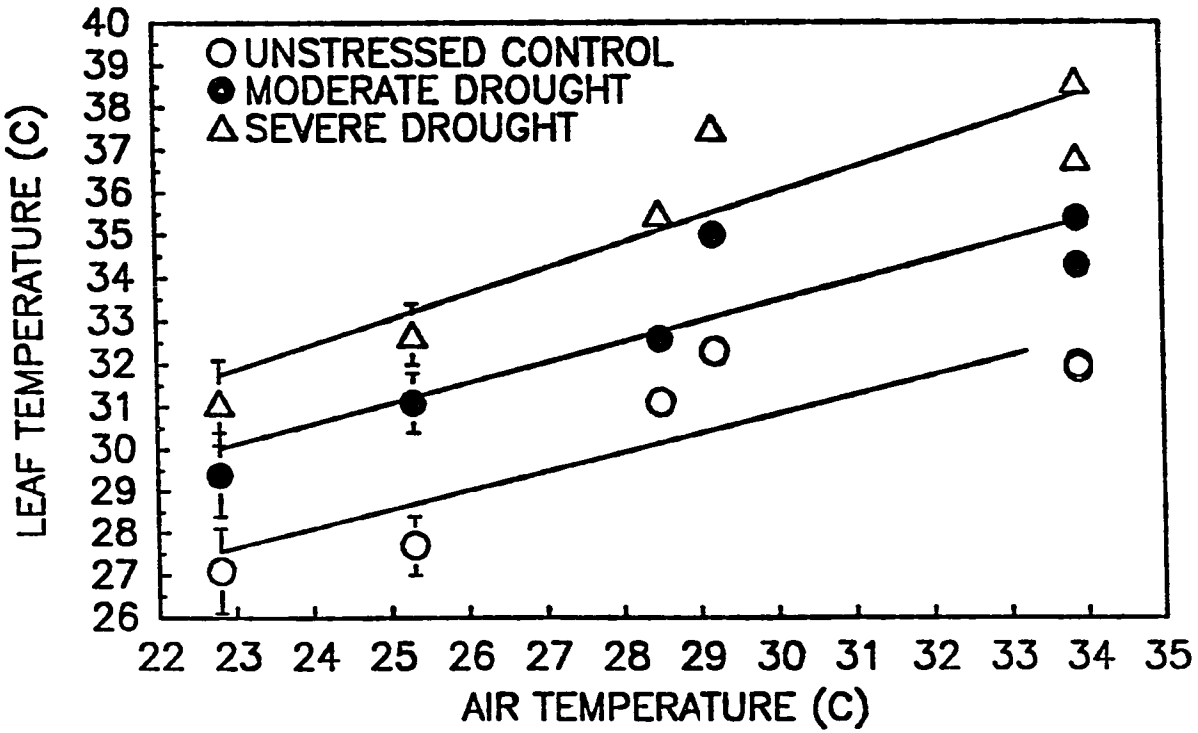


Figure 3. Actual temperature values of terminal, fully-expanded soybean leaflets at air temperatures of 20 to 35 C and three drought stress levels

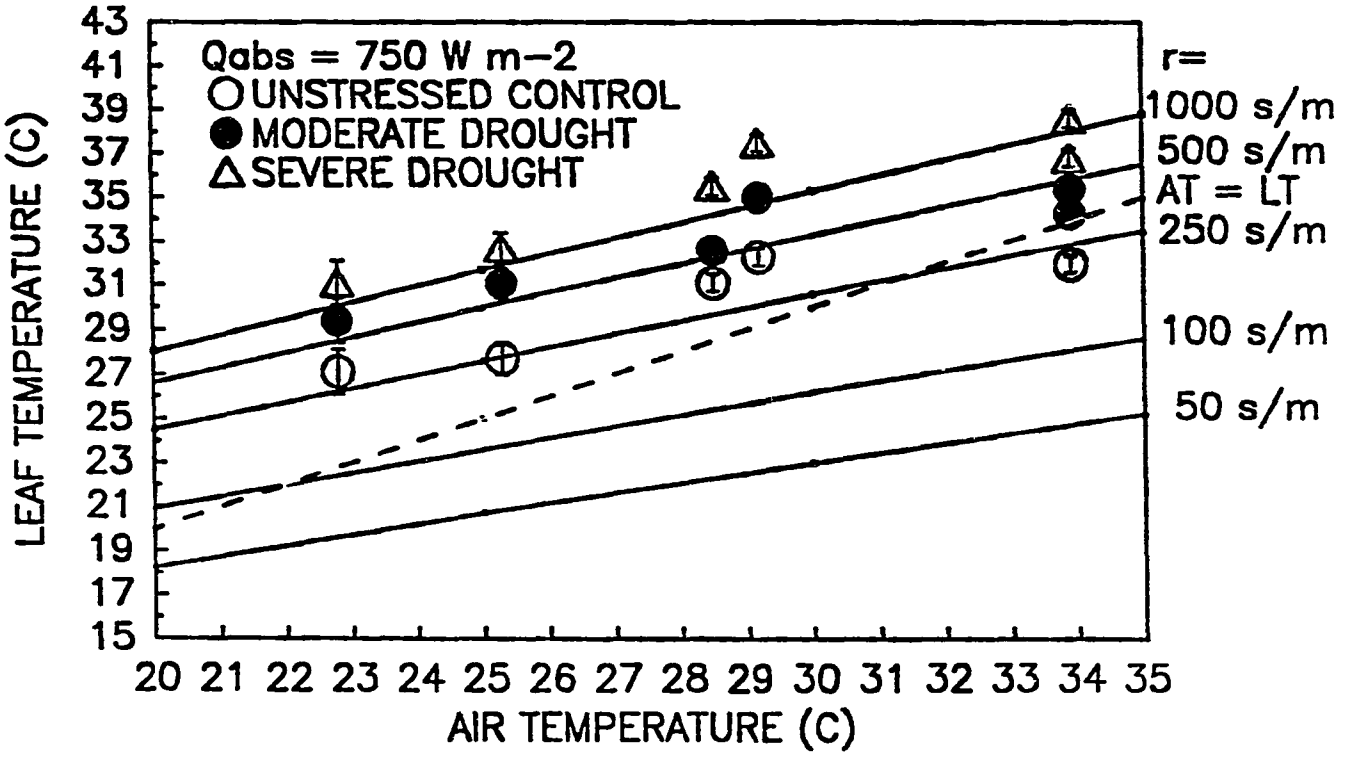


Figure 4. Comparison of predicted and empirically-measured leaf temperatures as a function of air temperature and drought stress

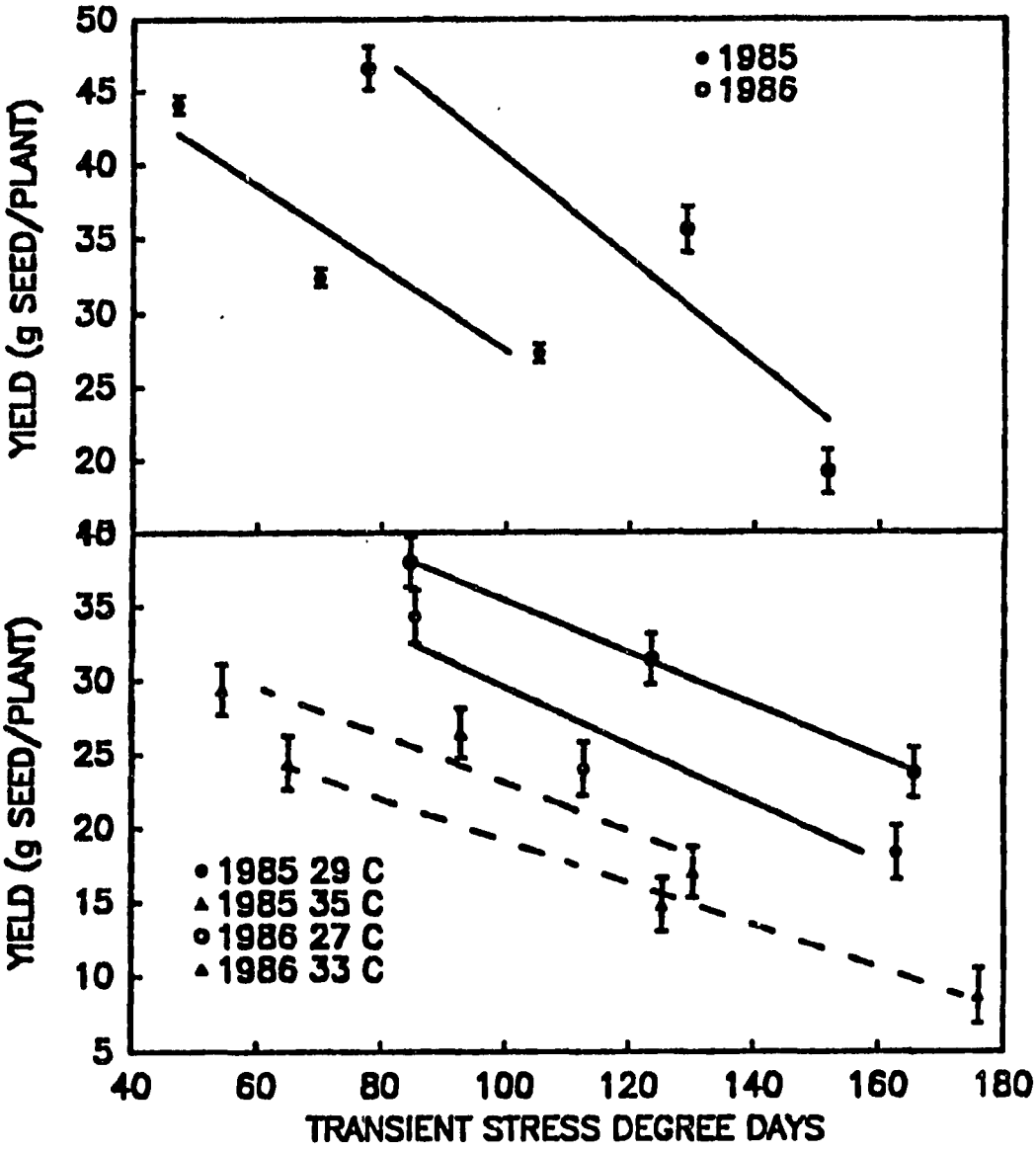


Figure 5. Yield of 'Gnome' and 'Hodgson 78' soybeans compared to the number of transient stress degree days (SDD) that accumulated during seed fill in 1985 and 1986

PAPER 4. DROUGHT AND HIGH TEMPERATURE STRESS EFFECTS ON SOYBEAN SEED PROTEIN AND OIL CONTENT, AND FATTY ACID COMPOSITION

Abstract

The effect of environmental stress during seed fill on soybean (Glycine max (L.) Merr.) seed chemical composition has received little attention. The objective of this study was to determine the effect of drought at several air temperatures (AT) on protein and oil content, and fatty acid composition. Drought stress was imposed on potted 'Gnome' soybeans at AT of 20 and 26 C, and 'Hodgson 78' soybeans at 29 and 35 C in 1985, and 27 and 33 C in 1986 in the greenhouse between R5 and R7. Oil content of seeds from well-watered plants increased with AT from 20 to 29 C, but decreased when AT increased to 35 C. Protein and oil content were inversely correlated (r= -0.87). Maximum oil and minimum protein content was 24.6% and 38.0%, respectively, in seeds from well-watered plants at 29 C. Oil percentage decreased and protein increased linearly by 3 to 5% because of severe drought. In 1985, protein content increased by 5.0 and 5.6 percentage points because of severe drought at 29 and 35 C, respectively, and oil decreased by 2.5 and 5.9 percentage points. Fatty acid

composition was altered more by AT than drought. Across years, an AT increase from 28 to 34 C reduced linolenic and linoleic acid 19 and 5%, respectively. Stearic and oleic acid content increased 15 and 13%, respectively. Linolenic acid was correlated with linoleic acid (r= 0.88) and with oleic acid (r= -0.87). Both high AT and drought altered soybean seed chemical composition and therefore oil quality and utilization properties, and should be considered in breeding efforts and grain marketing programs.

Additional index words: Environmental Stress, Fatty Acid Composition, Linoleate, Linolenate, Oil, Oleate, Palmitate, Protein, Stearate.

Introduction

Soybean grain is valued commercially for its edible oil and protein meal. Soybean seeds contain approximately 42% protein, 23% oil, 9% soluble carbohydrate, 5% pentosans, 5% crude fiber, and 16% hemicellulose at maturity (Bils and Howell, 1963). Protein and oil content exhibit a strong inverse correlation.

Air temperature (AT) can affect seed protein and oil content, but the effect of drought has not been reported.

Dillman and Hopper (1943) and Green (1986) found that flaxseed oil was negatively correlated with AT. With sunflower, increased AT has been shown to increase (Unger and Thompson, 1982) and decrease (Harris et al., 1978) oil, to give maximum oil content at 21 C (Canvin, 1965), and not to affect protein or oil content (Robertson et al., 1979). Seiler (1983) found no relationship between sunflower seed oil content and AT or solar-radiation intensity, but rather with daylength. Weiss et al. (1952) found soybean seed oil content was positively correlated with mean AT during seed fill. Howell and Cartter (1958) measured oil percentages of 23.2, 20.8, and 19.5% in soybean seeds that developed at day AT of 29.4, 25.0, and 21.1 C, respectively. Neither yield or protein content were affected by AT. AT during the 20- to 40-day period before maturity, when the majority of oil accumulated, was best correlated to oil content.

AT can affect the fatty acid composition of the seed oil, but the effect of drought is unknown. The fatty acid composition of mature 'Williams 79' soybean seed oil was 11.1, 4.2, 25.5, 53.2, and 6.0% of palmitate (16:0), stearate (18:0), oleate (18:1), linoleate (18:2), and linolenate (18:3), respectively (Dornbos and McDonald, 1986). Howell and Collins (1957) found high AT during seed fill decreased 18:3 content. Cramer and Beversdorf (1984)

found the soybean genotype interacted with the environment to produce low 18:3 content. Carver et al. (1986) reported that several environmental factors were responsible for changes in the proportion of unsaturated fatty acids in soybean oil. Maximum and minimum AT explained 84 and 69% of the variability in fatty acid composition, respectively. Green (1986) demonstrated with flaxseed oil that 18:2 and 18:3 percent decreased as AT increased, because oleate desaturase activity was inhibited by high AT. AT affected 18:3 content less in lines selected for low 18:3.

The effect of drought on soybean seed protein and oil content, and fatty acid composition, is unknown. AT can affect seed chemical composition in a variety of ways. Part of the variability in AT effects may be due to the effect of drought accompanying AT differences. The objective of this study was to determine the effect of several drought stress levels at a wide range of AT during seed fill on seed protein and oil content, and fatty acid composition.

Methods and Materials

Four experiments were conducted in 1985 and 1986. Determinate 'Gnome' soybean (Glycine max (L.) Merr.) plants

were produced in the first two experiments. Each of the 99 pots contained two plants at an AT of 20 C in 1985 (Experiment I), and one plant at an AT of 26 C in 1986 (Experiment II). Three drought stress treatments were imposed at R5 so that each of the three replications consisted of 11 plants.

One indeterminate 'Hodgson 78' soybean plant per pot was grown in each of 144 pots in 1985 (Experiment III) and 1986 (Experiment IV). All plants were debranched at R3. At R5, 72 pots were placed in one of two adjacent, similar greenhouse rooms. The daytime AT in these rooms were maintained at 29 and 35 C in 1985, and 27 and 33 C in 1986. Night AT was 19 C in both rooms. Three drought stress treatments were imposed so that each of the three replications consisted of 8 pots.

In both studies, the 7.6 L pots contained equal parts of soil, peat, and perlite. The plants were grown in the Agronomy greenhouse, Iowa State University, Ames, Iowa. Day/night AT of approximately 25/16 C with a 14 h photoperiod and adequate pot moisture were maintained until R5. Nitrogen, P, and K were applied at rates of 2.4, 1.3, and 2.4 g per pot, respectively, during alternate irrigations throughout plant development.

Drought stress was imposed on 'Gnome' and 'Hodgson 78'

plants by differential daily watering using trickle irrigation systems. The volume of water required to saturate unstressed control (well-watered) pots was delivered and measured daily, then 75 and 50% of that volume delivered for moderate and severe drought-stress treatments, respectively. Drought stress was quantified by calculating the stress degree day (SDD) values of each plant, the average difference between leaf and AT, as described by Dornbos (Paper 1, herein). The AT of each greenhouse room was measured continually using shielded hygrothermographs.

At R8, seeds from plants of both experiments were hand-harvested and bulked according to AT, drought and replication. Five- to seven-gram seed samples were removed randomly from each bulk and analyzed for protein and oil content using an infrared reflectance spectrophotometer at the USDA/ARS Northern Regional Research Center, Peoria, Illinois.

Fatty acid composition of the total seed oil from each treatment group was determined by gas chromatography. Five-seed samples were dried in a vacuum oven at 0.7 MPa and 85 C for approximately 15 h, then crushed using a hydraulic press at 1055 kg cm^{-1}. The total oil was extracted by soaking the seed material in 3 ml of distilled

hexane for 48 h, then 0.2 ml of the extract placed in a 2 ml glass vial. Fatty acid methyl esters were prepared by addition of 0.5 ml of 1 N sodium methoxide in methanol and allowed to react for 1.5 h. The transesterification reaction was stopped by addition of distilled water. The esters were partitioned from the reaction mixture by addition of 1 ml hexane. Approximately 1 h was allowed for the esters to partition into the hexane layer. Approximately 1.5 mg of fatty acid esters in hexane were separated on a Beckman GC-5 gas chromatograph equipped with a 2 m x 3.2 mm I.D. glass column packed with 15% EGSSX on Chromosorb W (100/120 mesh) at 185 C. Nitrogen gas (40 ml min^{-1}) was used as the carrier. Fatty acids were detected by flame ionization with hydrogen gas and flowrates of 50 and 300 ml min^{-1}, respectively. Fatty acid ester retention times were identified by comparison with authentic standards. Significance of treatment effects were tested by analysis of variance procedures.

Results and Discussion

The oil content of 'Hodgson 78' soybeans decreased 2.6 percentage points in 1985 and 0.4 percentage points in 1986 because the AT increased during seed fill (Fig. 1). In contrast, protein content increased 4.1 percentage points

in 1985 and 2.0 percentage points in 1986 because of increased AT. Oil and protein percent were correlated with AT (r= -0.35 and 0.55). Protein and oil content exhibited a strong inverse relationship (r= -0.88).

Howell and Cartter (1953, 1958) reported that oil content increased with AT, while protein content did not change, in contrast to our results. Soybean seed oil percentage was positively correlated with AT for five Maturity Group 0 varieties grown for one to three years at eight locations, and for six Group VIII varieties grown for two or three years at nine locations (Howell and Cartter, 1953). In growth chambers, Howell and Cartter (1958) found seed oil content increased linearly 3.7% when daytime maximum AT increased from 21.1 to 29.4 C, but yield, protein, and non-protein nitrogen were unaffected.

The maximum AT of 29.4 C used by Howell and Cartter (1958) corresponded to the minimum AT of 29 C for 'Hodgson 78'. Therefore, our data represented a different AT range than that reported by Howell and Cartter (1958). The protein and oil percentages of seeds from well-watered soybean plants of Experiments I, II, III, and IV were plotted with the oil percentages reported by Howell and Cartter (1958) against the daytime AT (Fig. 2), effectively extending the AT range reported earlier. Oil content

increased when daytime ATs increased between 20 and 29 C, and decreased between 29 and 35 C. Protein content changed inversely to oil. These data suggest a critical temperature existed near 29 C for maximum oil and minimum protein content. Canvin (1965) reported a similar relationship with sunflower oil content and AT.

Drought during seed fill increased soybean seed protein and reduced oil content at each AT with both cultivars. Protein content of 'Gnome' seeds increased linearly 4.7 percentage points, and oil decreased 2.5 percentage points, because of severe drought (Fig. 3). Similarly, protein content of 'Hodgson 78' seeds increased linearly 3.5 percentage points, and oil decreased 1.9 percentage points, because of severe drought at 28 C (Fig. 4). At 34 C, 'Hodgson 78' protein content increased linearly 4.9 percentage points, whereas oil content decreased 4.4 percentage points, because of severe drought. In contrast, Hurburgh et al. (1985) found oil content was higher, and protein lower, in grain samples obtained from storage elevators located in dry areas of Iowa in 1983 and 1984. Protein and oil content may have been affected by AT differences in addition to drought, accounting for the different trends attributed to drought.

In 1985, but not 1986, AT and drought interacted to

affect protein and oil content. Protein content increased 0.6 percentage points more because of severe drought at 35 than at 29 C (Fig. 4). Conversely, oil content decreased 3.4 percentage points more because of severe drought at the higher AT. Drought and AT also interacted in 1985 for SDD, yield, seed mass, viability, and vigor, but not in 1986 (Paper 2, herein).

High AT reduced the percentage of linoleate (18:2) and linolenate (18:3), and increased oleate (18:1) proportionately. Across years, the 18:3 content of 'Hodgson 78' seeds was reduced 19% by an increase in AT from 28 to 34 C (Table 1). 18:0 and 18:1 content increased, and 18:2 decreased, because of high AT in 1985. In 1986, only 18:1 increased significantly, but 18:0 and 18:2 followed the same trends as the previous year. The 4.1 percentage point decrease in 18:2 and 18:3 was nearly compensated for by the 3.7 percentage point increase in 18:1. 18:3 percentage exhibited correlation coefficients of 0.66, -0.83, and -0.59 with 18:2, 18:1, and 18:0 percentages, respectively. Howell and Collins (1957) also found increased AT conferred lower 18:3 content in soybean. The minimum and maximum AT was correlated with 18:3 content by -0.85 and -0.80, respectively (Carver et al., 1986).

Green (1986) found a positive correlation with 18:2,

18:3, and elevated AT, and a negative correlation with these fatty acids and 18:1 in flax. A reduction in oleic acid desaturase activity by high AT was responsible for the altered fatty acid composition. Wilson et al. (1980) demonstrated with developing soybean that 18:2 and 18:3 were synthesized by consecutive desaturation of 18:1. These data indirectly suggest that oleic acid desaturase activity was inhibited by high AT in soybean also. Seed fill at the stressfully-high AT increased the quantity of substrate (18:1) and decreased the quantity of the products (18:2 and 18:3) proportionately (Table 1).

The effect of drought on soybean seed oil fatty acid composition was significant, but less dramatic than the effect of AT. 18:3 content of 'Hodgson 78' seeds was unaffected by severe drought, but that of 'Gnome' seeds increased 12% (Table 1). In 1985 and 1986, 16:0 content of 'Gnome' seeds increased linearly, but did not change in 'Hodgson 78'. In 1985, 18:1 content of 'Gnome' seeds increased and 18:2 content decreased because of severe drought, but the opposite occurred in 1986. With 'Hodgson 78', 18:0 content increased in 1985, and 18:2 content decreased in 1986 because of severe drought. The significance of the changes in soybean seed fatty acid composition because of severe drought were unclear.

Conclusions

Soybean seed chemical composition was affected by AT and drought during seed fill. Protein and oil content exhibited minima and maxima, respectively, because of a critical AT near 29 C. Oil content decreased, and protein content increased, linearly because of increased drought, the rate of change being dependent upon AT in 1985. Linoleic and linolenic acid content decreased, while stearic and oleic acid content increased proportionately, because of an increase in AT from 28 to 34 C across years. Drought had a small effect on soybean oil fatty acid composition. Attention should be paid to the environmental conditions that occur during seed fill because these parameters can affect seed composition. Compositional variation because of these environmental parameters could have important implications in breeding and grain marketing programs, and utilization properties.

Table 1. Fatty acid composition of 'Hodgson 78' and 'Gnome' soybeans exposed to drought and high temperature stress throughout seed fill and averaged across 1985 and 1986

Air Temperature (C)	Drought Stress (SDD)	16:0[a]	18:0[b]	18:1[c]	18:2[d]	18:3[e]
		%				
		'Gnome'				
23	53.4	10.8	3.4	26.1	51.6	8.0
	101.3	10.5	3.3	26.2	51.5	8.1
	140.6	10.3	3.4	26.5	51.0	8.5
	SE	0.2	0.1	0.6	0.5	0.2

[a]Palmitic acid.

[b]Stearic acid.

[c]Oleic acid.

[d]Linoleic acid.

[e]Linolenic acid.

Table 1. continued

Air Temperature (C)	Drought Stress (SDD)	16:0	18:0	18:1	18:2	18:3
		---------- % ----------				
		'Hodgson 78'				
28	32.3	11.8	3.6	24.6	53.2	6.9
	55.0	11.8	3.5	24.7	53.2	6.9
	84.4	11.8	3.5	25.2	52.7	7.0
	SE	0.2	0.1	0.6	0.5	0.2
34	-21.7	11.5	4.0	27.7	51.4	5.6
	9.7	11.5	4.2	28.4	50.4	5.6
	40.8	11.6	4.2	29.3	49.3	5.7
	SE	0.2	0.1	0.6	0.5	0.2

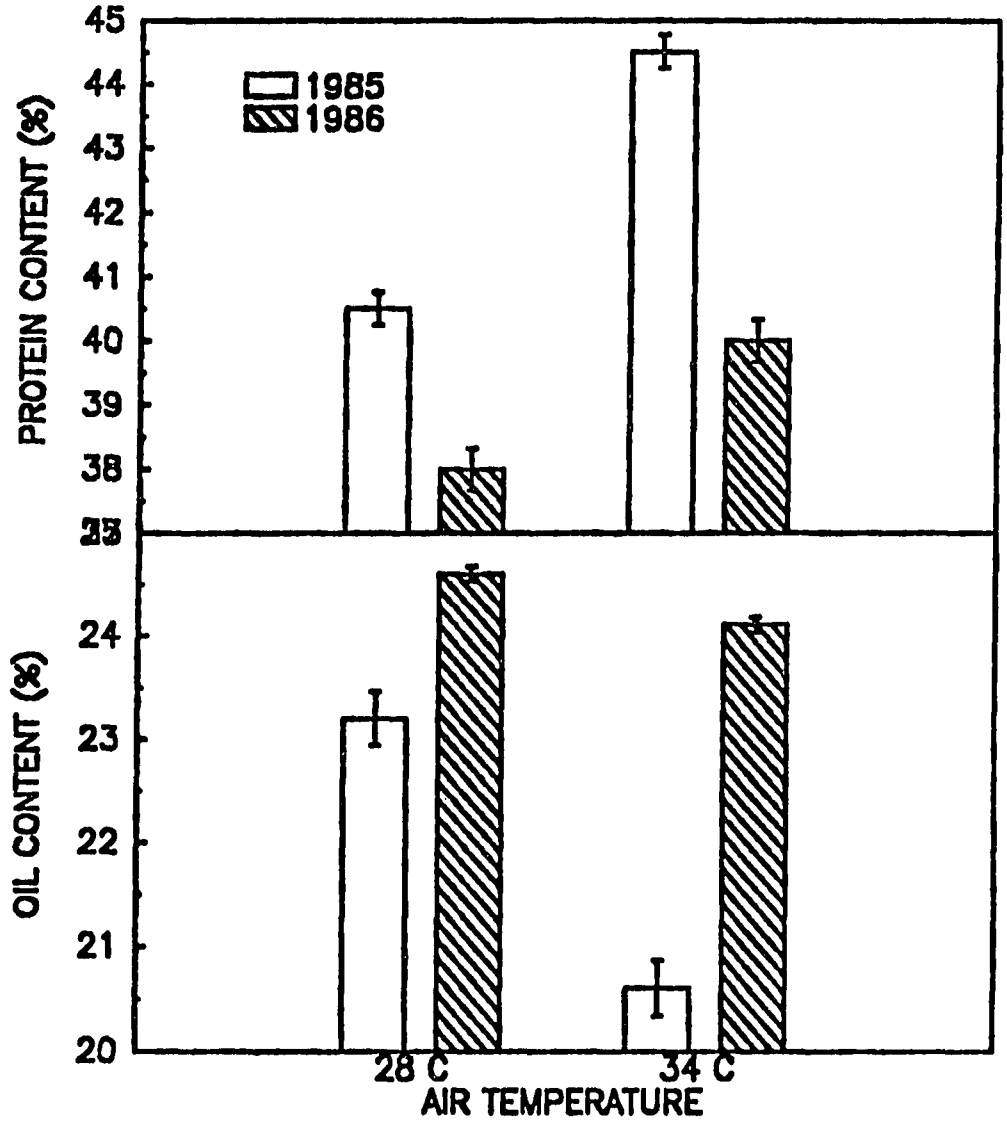


Figure 1. Protein and oil content of 'Hodgson 78' soybean seeds that developed at an optimum or stressfully-high air temperature in 1985 and 1986

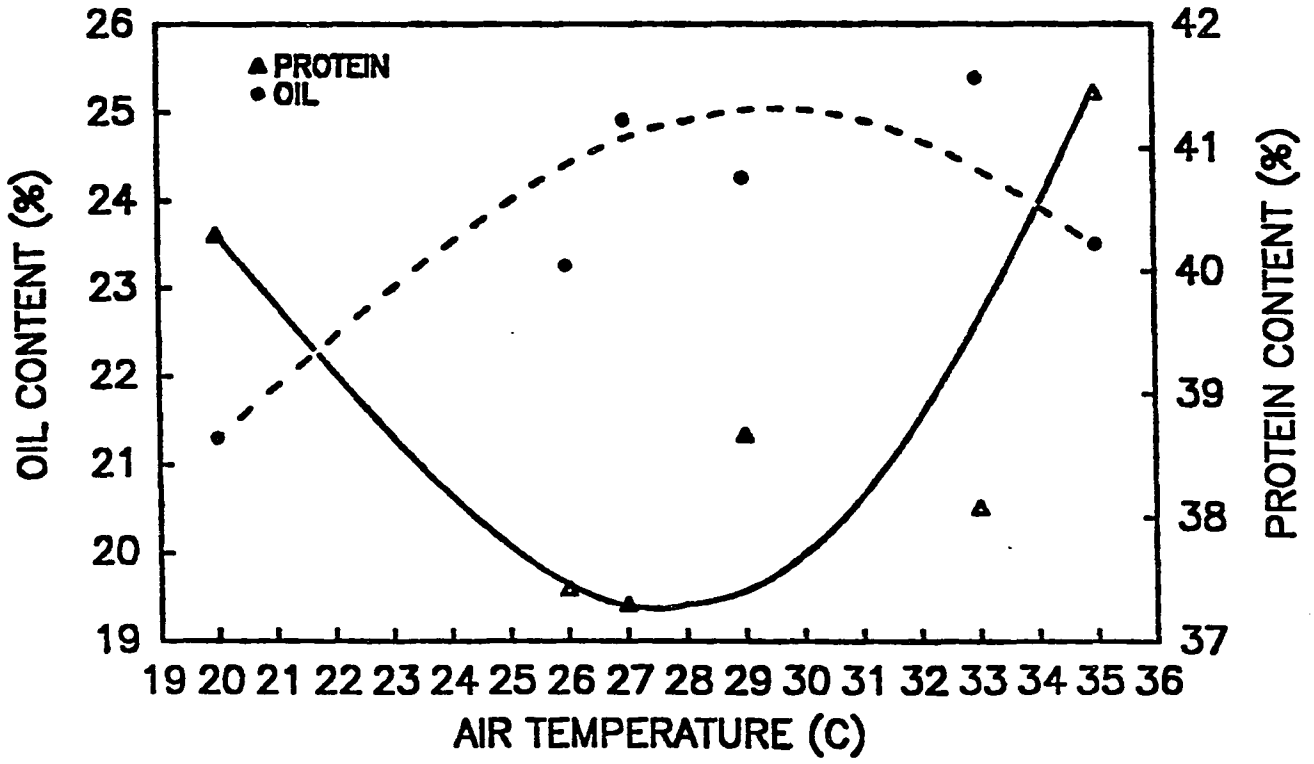


Figure 2. Protein and oil content as a function of air temperature during soybean seed development, with Howell and Cartters (1953) oil content data plotted for reference

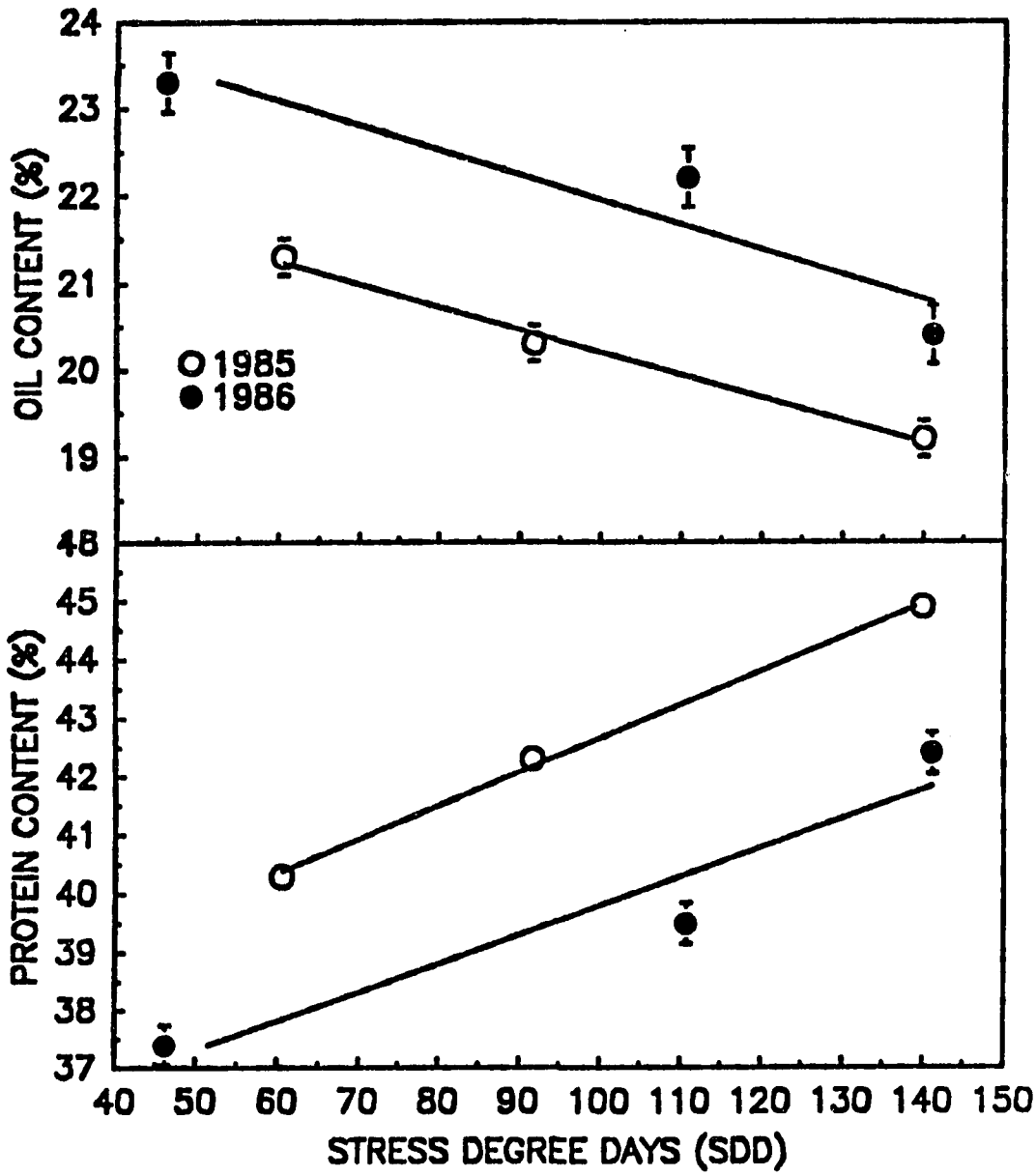


Figure 3. Protein and oil content of 'Gnome' soybean seeds that were exposed to three drought stress levels during seed fill in 1985 and 1986

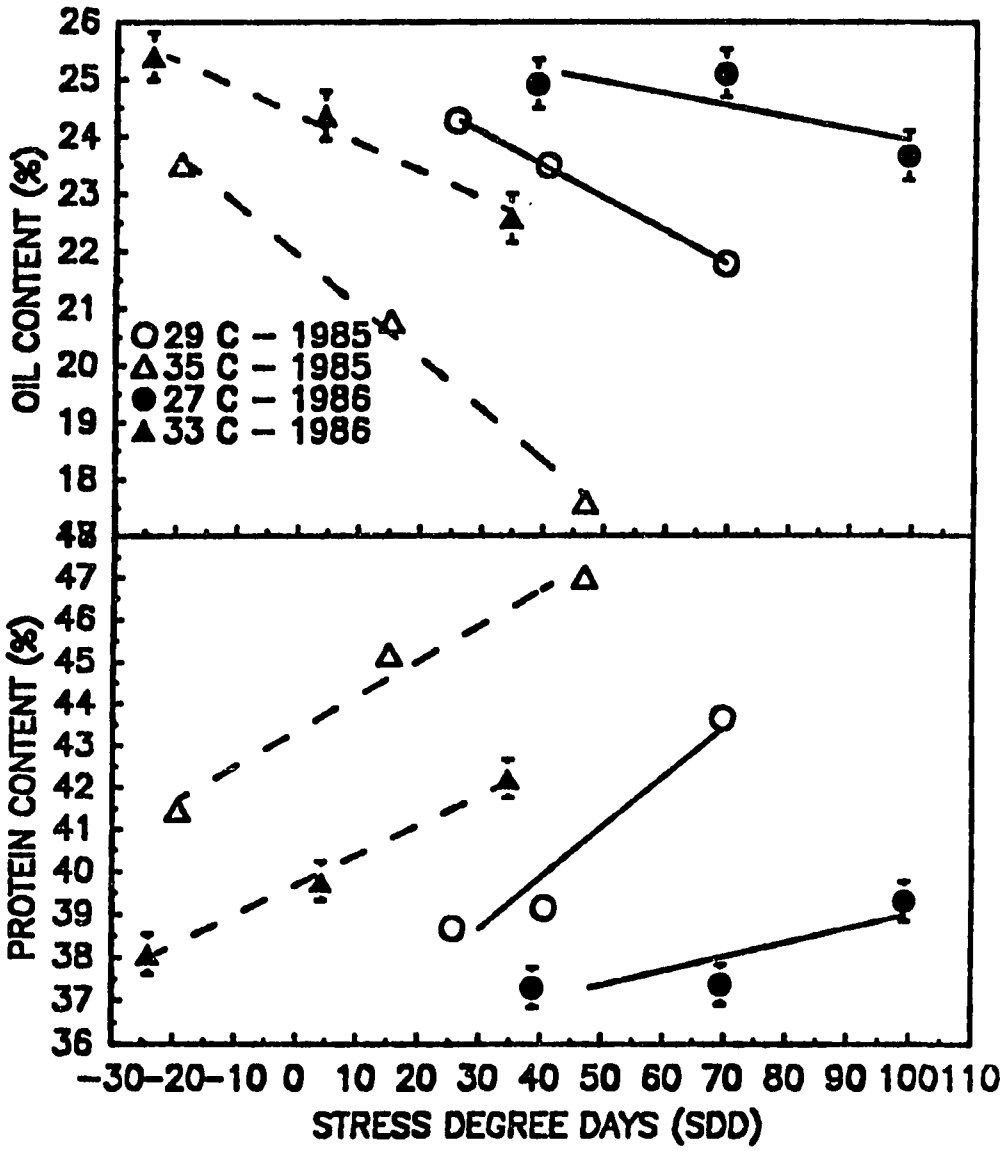


Figure 4. Protein and oil content of 'Hodgson 78' soybean seeds that were exposed to three drought stress levels at an optimum or stressfully-high air temperature during seed fill in 1985 and 1986

PAPER 5. EFFECT OF HIGH TEMPERATURE ON SEED PHOSPHOLIPID COMPOSITION, VIABILITY, AND VIGOR: A REVIEW

Introduction

Environmental stress during seed fill can reduce seed viability and vigor, and alter the seed chemical composition (Papers 1 and 2, herein). Excess solute leakage from seeds is one manifestation indicating reduced vigor because of high air temperature (AT) during seed fill. Loss of membrane integrity has been postulated as the first deleterious step in the progressive process of seed deterioration, eventually culminating in vigor loss (DeLouche and Baskin, 1973). The biochemical and physiological basis associated with seed quality loss is unknown (TeKrony, 1980).

A number of laboratory tests are available to the seed technologist to determine seed lot quality (AOSA, 1983). These tests are correlated with field performance, but the physiological causes of reduced vigor are unknown. It would be useful to understand the physiological mechanism of seed quality loss, and therefore the rationale for the correlation with field and laboratory measures of seed viability and vigor.

Because these tests are correlated with field

performance, they provide an opportunity to study the physiology of the deterioration process. The conductivity test, one laboratory test used to estimate seed vigor, represents an assessment of seed leakiness. Excessive leakage from seeds is an indication of poor physical condition which predisposes the seed to soil-borne pathogens (Matthews and Bradnock, 1967).

Seeds that leak a large proportion of their solutes exhibit reduced vigor (AOSA, 1983), presumably because of reduced membrane integrity (Simon, 1974). High AT during soybean seed fill increases seed conductivity (Paper 1, herein). AT also interacts with membrane lipid composition, determining whether a membrane is fluid or leaky at a particular AT (Thompson, 1980a). The effect of the seed fill and germination AT on membrane lipid composition, fluidity, and leakage may provide a physiological explanation for seed vigor loss.

The objectives of this review were: First, to propose a physiological mechanism describing how high AT during seed fill could reduce seed viability and vigor by its effects on membrane lipid composition. Second, to demonstrate the relationship between AT and membrane lipid composition of microorganism and plant tissues. And third, to relate the composition of seed membrane lipids resulting from a seed fill environment where the AT was high to membrane fluidity

and functionality in a cool germination environment.

A Model Relating High Temperature, Phospholipid Composition, and Reduced Vigor

Phospholipid composition is dynamically controlled in response to environmental conditions. In time, phospholipid composition is optimized to a given set of environmental conditions. Phospholipid composition interacts with the environment to determine membrane fluidity. If membrane lipid composition is well suited to the existing conditions, then the membranes will exhibit optimum fluidity. A change in environmental conditions confers reduced membrane fluidity, and therefore increased leakage of cell solutes and reduced activity of membrane-bound enzymes.

Seeds that develop at a high AT contain membrane phospholipids whose composition is optimized for the maintenance of fluid membranes and metabolic activity at the high AT. While representing an advantage for the developing seed at the high AT by allowing the maintenance of growth, this same phospholipid composition represents a disadvantage in a typical germination environment in which the seedbed is relatively cool. During imbibition, the membranes of seeds adapted to the high AT would exhibit

poorer fluidity and increased leakiness to cell solutes, relative to adapted membrane lipids. Excess leakage during imbibition, and high conductivity measures, is then indicative of reduced vigor because of poor membrane fluidity. One mechanism for reduced vigor, therefore, may be the presence of seed membrane lipids that are not sufficiently adapted to the germination environment resulting in increased solute leakage during imbibition.

Membrane Composition and Properties of Phospholipids

Membranes are composed of protein and lipid molecules arranged in a highly ordered bilayer. The majority of membrane lipid is phospholipid (Erwin, 1973; Thompson, 1982). The composition of membrane phospholipids is complex. Variation exists in the quantity of phospholipid, the phospholipid class composition, and the fatty acid composition of each class (Chapman, 1983). Other polar lipids, such as glycolipid and sulfolipid, are important in some membranes (Erwin, 1973). In mature soybean seed, Wilson and Rinne (1974) measured 46.0, 25.0, 17.4, and 3.6% phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylinositol (PI), and phosphatidylglycerol (PG), respectively, comprising 84% of the total.

Phospholipids exhibit a thermal mesomorphism upon

heating. This endothermic process drives phase changes from a gel to liquid-crystalline to liquid upon heating (Chapman, 1983). Water is readily absorbed by phospholipid, ten water molecules being bound per phospholipid molecule. Water interacts with the molecules to reduce the quantity of heat required for phase transition. The phase a given membrane is in depends upon its composition, the AT of the medium, and its degree of hydration.

Membrane fluidity is determined by AT, degree of hydration, phospholipid head group composition, and fatty acid chain length and degree of unsaturation. Membrane lipid composition of Tetrahymena pyriformis was heterogeneous and dynamically regulated in response to AT (Thompson, 1980a). A transition can occur from the liquid-crystalline (fluid) phase to the gel (rigid and leaky) phase, as the AT and/or degree of hydration is reduced. Relatively small changes in membrane lipid composition can change the transition AT dramatically, altering membrane physical properties (Thompson, 1980a). Therefore, AT, water content, and phospholipid composition interact dynamically to determine the fluidity of a membrane for a particular set of environmental conditions.

Effect of Temperature on Phospholipid Composition

Research conducted with microorganisms has demonstrated that phospholipid composition is regulated in response to AT (Thompson, 1980a) to maintain optimum membrane fluidity and functionality (Sinensky, 1974). Failure to maintain optimum fluidity impairs the barrier function of the membranes; that is, their ability to maintain proton and chemiosmotic gradients and to prevent the leakage of solutes from cells (Silvius et al., 1980). Wilson and Barran (1980) described four ways that membrane composition can change in response to a change in AT: 1) degree of fatty acid unsaturation, 2) fatty acid chain length and degree of branching, 3) phospholipid class composition, and 4) sterol content. Each resulted in improved fluidity at the new AT.

The potential and rate of change of phospholipid composition is well known with microorganisms. When Tetrahymena pyriformis was transferred from 39.5 to 15.0 C, linoleic and linolenic acid percentages increased and palmitic acid decreased within 30 m (Thompson, 1980b). Fukushima et al. (1979) found that the quantity and activity of palmitoyl-CoA desaturase increased 400% during the first few minutes of cold AT acclimation. When the AT decreased from 35 to 20 C, decreased membrane fluidity stimulated desaturase activity, causing the irreversible

desaturation of existing fatty acids in Bacillus licheniformis from a saturation:unsaturation ratio of 20:1 to 2:1 (Fulco and Fujii, 1980). Supra-optimum fluidity occurred when AT increased from 0 to 20 C with Micrococcus cryophilis, and stimulated the activity of a fatty acid elongase (Russell and Sandercock, 1980). In Fusarium oxysporum, Wilson and Barran (1980) observed that the PE:PC ratio decreased when AT increased from 15 to 37 C. Microorganism phospholipid composition exhibited great potential for change when AT changed.

Little research has been conducted with plant membrane lipids relating membrane lipid composition, fluidity, and functionality in response to environmental stress. Pike (1982) found the ability of plants to acclimate to AT change was partial and variable with genotype. In chilling-sensitive plants, growth ceased between 0 and 12 C whereas chilling-tolerant plants could continue to grow (Lyons et al., 1979). Thompson (1980a) and Roughan (1985) related increased fatty acid desaturation with decreased AT in vegetative growth of chilling-tolerant species. In chilling-resistant rye and wheat, enhanced desaturase activity gave rise to increased linolenic acid content (Thompson, 1980a). Phospholipid content doubled because of cool AT. Pike (1982) extracted phospholipids from cool-season annuals and measured a lower membrane order/disorder

transition AT presumably because of the lower melting AT of the polyunsaturated fatty acids than for warm-season annuals. Increased unsaturation decreased the phase transition AT allowing membranes to remain fluid at lower AT. These changes maintained fluid membranes in cool environments allowing maintenance of barrier and membrane-bound enzyme activities (Pike, 1982).

Liposome vesicles, reconstructed from total seed lipids and mitochondrial membranes from soybean seeds, indicates that low AT does not cause chilling damage by inducing a bulk phase transition in the membrane lipids (O'Neill and Leopold, 1982). Pike (1982) suggested a small portion of the membrane lipid might undergo a phase transition. Nakatani and Barber (1977) observed that even if as little as 1% of the membrane fatty acid was saturated (primarily acylated to PG), a thermal phase transition was detectable. Disaturated PG accounted for less than 25% of the total PG in chilling-resistant plant leaves, but 50 to 60% in most chilling-sensitive plants (Roughan, 1985). Murata et al. (1982) measured a higher 16:0/16:1 ratio in PG of chilling-sensitive than resistant plants. Lyons et al. (1979) correlated chilling sensitivity, abnormal membranes, and membrane-bound enzyme function with reversible lipid-phase separation in cellular membranes. Therefore, even a small proportion of the total membrane lipid can cause a local

phase transition, resulting in decreased membrane and enzyme function, increased leakiness, decreased metabolism, and chilling-sensitivity.

Changes in AT caused the phospholipid composition of microorganisms and plants to change similarly. Elevated AT causes the quantity of phospholipid and PE to decrease, and the fatty acid composition to shift toward longer and more saturated carbon chains.

Phospholipid Composition and Seed Germination

Optimum membrane fluidity can be maintained in developing seeds by dynamic regulation of membrane lipid composition. The phospholipid composition of a seed exposed to high AT during seed fill would be conducive to the maintenance of fluid and functional membranes. Consistent with microorganism data, preliminary evidence indicates that soybean seeds that developed at stressfully-high ATs contain less phospholipid, PE, linoleic and linolenic acid than those that develop at optimum ATs. These changes reflect an adaptation to prevent the formation of the lethal hexagonal phase upon dehydration (J. H. Crowe, Department of Biochemistry, The Univ. of Calif.-Davis, personal communication).

Removal of hydration water from membrane lipids reduces

the transition AT from the gel to liquid-crystalline phase greatly. This transition causes bilayers to become leaky, lateral phase separation of the phospholipids to occur, and non-bilayer phases such as the lethal hexagonal phase to form (Crowe, personal communication). Crowe et al. (1987) demonstrated with PE systems that the insertion of sugars and PC prevent the formation of the hexagonal phase in organisms that usually survive dehydration by blocking the formation of bonds between adjacent ethanolamine head-groups. The transition AT is thereby effectively lowered so that the dehydrated membranes remain in the liquid-crystalline phase. Therefore, the changes in the phospholipid composition of microorganisms and soybean seeds grown at high AT reflect an adaptation allowing survival from dehydration at a high AT.

The first step in the germination process is imbibition. Imbibition is the biophysical process of water absorption. Solute efflux, or imbibitional damage, occurs as a consequence of water absorption in all dry organisms, including seeds, spores, pollen grains, and some nematodes (Simon, 1974). The rate of solute leakage from pea embryos is very rapid for the first several minutes of imbibition, but rapidly declined to slow rates after 30 to 60 m. The material leaking from seeds originated from within the cells constituting the seeds (Simon and Raja Harun, 1972),

and consisted of twenty-two amino acids, glucose, fructose, sucrose, maltose, organic acids, gibberellic acid, fluorescent materials, phenolics and phosphates (Simon, 1974). The slowed leakage rate was postulated to be the result of leakage cessation of peripheral cells that were fully hydrated, along with the commencement of leakage from internal cells just beginning to absorb water (Simon and Raja Harun, 1972).

Simon (1974) postulated there is a molecular mechanism for leakage from these and other data. The membranes of the constituent cells of dry seeds did not constitute effective barriers so that when placed in water, solutes rapidly diffused from the seeds. Upon hydration, the membranes rapidly changed from the porous hexagonal phase to the non-porous laminar phase thereby restricting solute loss. Membranes exhibiting the hexagonal arrangement of lipids have not been identified in living systems, however. Crowe et al. (1987) suggested that the solute leakiness by the bilayer likely is the consequence of a localized gel to liquid-crystalline phase transition.

While representing the optimum composition for growth and dehydration at a high AT, this membrane lipid composition is non-optimum for imbibition at a low AT. The phospholipids of seeds that developed at high AT would contain proportionally more saturated fatty acids because

their high melting temperature would confer optimum fluidity at the high AT. At a low AT, these phospholipids would not be as fluid, and would therefore require a longer period of time to make the transition from the gel to liquid-crystalling phase upon hydration.

Typically, the germination environment is cool and wet. Seeds that develop at a relatively high AT would be expected to leak greater quantities of solutes. In support, 'Hodgson 78' seeds exposed to an AT of 33 C during seed fill exhibited higher conductivity after soaking for 24 h at 25 C than seeds that developed at 27 C (Paper 2, herein). Membrane lipid composition and fluidity may therefore represent one mechanism of seed vigor loss because of environmental stress during seed fill.

Summary

Environmental stress during seed development can reduce seed vigor. Membrane lipid composition, and therefore fluidity, is regulated dynamically in response to AT. The membrane phospholipid composition that confers fluidity at a high AT may limit the ability of desiccated membrane lipids to undergo a phase transition from the leaky gel to the restrictive liquid-crystalline bilayer. A slower rate of transition could result in excess solute leakage conferring lower seed vigor.

PAPER 6. POD POSITION AND ENVIRONMENTAL STRESS EFFECTS ON POD TEMPERATURE AND SEED YIELD, QUALITY, AND COMPOSITION

Abstract

A greenhouse study was conducted to relate drought and pod temperature at three pod positions to soybean yield components, viability and vigor, and chemical composition of a determinate and indeterminate soybean (Glycine max (L.) Merr.) cultivar. Thermocouples, inserted into pods from upper and lower nodal positions at R5, measured pod temperature hourly. Drought was imposed at a wide range of air temperatures (AT) by delivering differing volumes of water to potted plants. For 'Hodgson 78', pod temperature exhibited a maximum of 26.5 C between 900 and 1500 h. At 1400 h, pod temperature was 1.4 C warmer at top than bottom positions but did not vary with drought. The mass, viability, and vigor of seeds from the top positions of the determinate cultivar were less than those from bottom positions. The position effect was exacerbated by drought and high AT. Protein content of seeds from bottom positions was 1.4 percentage points higher, oil was 2.6 percentage points lower, and linoleic and linolenic acid was lower than those from bottom positions for determinate and indeterminate cultivars. Seed mass, viability, and

vigor reflected growth habit differences, whereas composition reflected pod temperature. Differences between pod positions for these traits should be considered in breeding and modelling programs.

Introduction

The position at which a soybean pod develops on the parent plant can exert an effect on seed characteristics such as the yield components, viability, vigor, and chemical composition. Position effects have been attributed to differences in growth habit and to microclimatic factors. Position effects may vary in response to drought during seed fill; Wallace (1986) found yield of field-grown determinate soybeans from upper strata was increased by irrigation because of greater seed mass and number per pod.

Egli et al. (1978) demonstrated that indeterminate soybean seeds from top plant positions had longer fill duration, unchanged fill rate, and greater mass than bottom positions. Ramseur et al. (1984b) and Wallace (1986) found that less yield and fewer seed numbers, but greater seed mass, was associated with the upper stratum of irrigated and non-irrigated determinate 'Braxton' soybeans. Adam (1983) found that seeds from the top half of an indeterminate cultivar had greater seed dry weight,

standard and accelerated aging germination percentage, and seedling growth rate. The effect of position, and its interaction with environmental stress, on seed viability and vigor was unknown.

Pod position on the plant affects seed mass and chemical composition. Collins and Cartter (1956) found that soybean seeds from the lower half of the plant contained 0.5% more oil and 1.0% less protein. Seeds from terminal pods of determinate soybean racemes contained 2.0% less oil, and terminal seeds within a pod contained slightly more oil.

High AT during seed fill contributed to reduced yield, because fewer and smaller seeds were produced, and to reduced viability and vigor (Paper 2, herein). Protein content increased, oil content decreased, and linoleic and linolenic acid content decreased when seed development occurred at 34 C as opposed to 28 C (Paper 4, herein). AT is vertically stratified within a crop canopy. Higher ATs are associated with upper strata because irradiated leaves are warmer than shaded leaves and therefore they conduct and convect more thermal energy to the air surrounding those leaves. It has not been shown, however, whether AT differences within a canopy relate to pod temperature differences.

The objectives of this study were to: First, measure

pod temperature at upper and lower canopy strata. Second, measure yield component, seed viability and vigor, protein and oil content, and fatty acid composition of seeds from three pod positions of a determinate cultivar, and from two pod positions of an indeterminate cultivar.

Methods and Materials

Determinate 'Gnome' and indeterminate 'Hodgson 78' soybeans plants were grown in the greenhouse as described by Dornbos (Papers 1 and 2, herein). After harvest maturity (R8), each 'Gnome' plant was divided into three positions: top and bottom halves of the of the pod-bearing nodes from the main stem, and branches. 'Hodgson 78' plants were debranched at R2. After R8, these plants were divided into top and bottom halves of the main stem as before.

The seeds from each drought, AT, and pod position treatment were hand-harvested, counted, and weighed for yield component analysis. Random samples were removed from each seed lot for determination of seed viability, vigor, and chemical composition. The standard germination, relative growth rate, and conductivity tests were conducted as described in the Rules for Testing Seeds (AOSA, 1986) and Vigor Testing Handbook (AOSA, 1983). Protein and oil content, and fatty acid composition, were determined as

described by Dornbos (Paper 4, herein).

Pod temperature was determined by inserting thermocouples into the central locule of pods from 24 plants. From each plant, one full-sized pod from one of the uppermost three pod-bearing nodes and one pod from the third pod-bearing node from the plant base was selected. Pod temperature was measured hourly throughout the seed fill period using a Campbell Scientific CR21XL micrologger equipped with a thermocouple multiplexer. The pod temperature data were analyzed as a split-plot randomized complete block design with four replications and six plants per replication. Three drought stress levels were imposed as described by Dornbos (Papers 1 and 2, herein) and represented the main-plots. The two pod positions represented the split-plots.

Results and Discussion

Pod temperature varied diurnally with AT, exhibiting a maximum between 900 and 1800 h (Fig. 1). Pods from top positions were warmer than those from bottom positions throughout the period of maximum temperature, being 1.4 C warmer at 1400 h. The temperature of pods from both positions were similar between 1900 and 800 h (during the evening) each day (data not shown). Drought stress did not significantly affect pod temperature at any time during

the seed fill period (Fig. 2). Similarly, there was no relationship between time of irrigation and pod temperature, suggesting that pod water relations were controlled independently of plant water relations.

Yield and the yield components of 'Gnome' differed among positions (Fig. 3). More yield was produced by the top position because more and larger seeds were produced in 1985. Significantly more yield was produced by branch positions in 1986 because of larger seed numbers. Yield between top and bottom positions did not differ, but seeds from top positions were larger. The yield distribution varied between years because two plants were grown per pot in 1985 and one per pot in 1986. The higher plant density of 1985 caused a larger proportion of the yield to be produced on the main stem. Egli et al. (1978) and Wallace (1986) found determinate soybeans that were irrigated produced larger seeds at upper strata even though the timing of seed fill initiation or termination did not vary with position or seed mass.

Drought reduced 'Gnome' yield, seed number, and seed mass from branch positions to a greater extent than from either main axis position in 1986 (Fig. 3). A SDD x position interaction for the yield components was not significant for 'Gnome' in 1985.

Greater yield and seed number of the indeterminate

soybean cultivar were produced at bottom positions both years (Fig. 4). Seed mass did not vary with position in 1985, but seeds from bottom positions were 8% larger in 1986 possibly because seed fill was initiated earlier. Seed mass varied differently with position for determinate and indeterminate cultivars.

Position interacted with SDD in 1985 to reduce 'Hodgson 78' yield and the mass of seeds from the top half of the main stem to a greater extent than bottom (Fig. 4). In 1986, the same interaction reduced yield from top positions because smaller and fewer seeds were produced. Similarly, Ramseur et al. (1984b) and Wallace (1986) found nonirrigated soybean plants produced larger seeds at lower strata than irrigated plants. A position x AT interaction was also significant in 1985 for reduced yield and seed number from bottom positions.

Seed viability and vigor was also dependent upon position. 'Gnome' seeds from top positions exhibited a 4.0 percentage point increase in standard germination percentage, a 3.7 mg per seedling increase in dry weight, and lower leachate conductivity in 1985 (Table 1). Seed quality did not interact with SDD either year. Seeds from the top position of the determinate cultivar 'Gnome' did exhibit greater viability and vigor in 1985 when the majority of yield was produced on the main stem. Higher

viability and vigor from top positions was associated with larger seed mass (Paper 1, herein).

Standard germination percentage and SADW of 'Hodgson 78' soybean seeds did not vary with position in 1985 or 1986 (Table 1). A SDD x position interaction was significant for germination percentage in 1985 as severe drought decreased the germination percentage of top and bottom seeds by 23 and 9%, respectively (data not shown). A position x SDD x AT interaction was significant in 1985 as SADW was reduced 37 and 15% at 35 C for top and bottom positions, respectively, and 6 and 5% at 29 C (data not shown). In contrast to determinate 'Gnome', top seeds of indeterminate 'Hodgson 78' exhibited lower viability and vigor because of environmental stress. These trends were consistent with the effects of stress and position on seed mass (Paper 2, herein). Neither seed mass nor viability and vigor were affected by position, but environmental stress interacted with position to reduce mass, viability, and vigor.

Protein and oil content varied with pod position similarly for determinate 'Gnome' and indeterminate 'Hodgson 78' soybean seeds. Seeds from the top half of the main stem of 'Gnome' soybeans contained 2.2 percentage points less protein than seeds from bottom positions in 1985, but did not differ in 1986 (Table 2). Inversely, 0.7

percentage points more oil was contained in top soybean seeds in 1986, but oil content did not differ in 1985. The chemical composition of seeds from branch positions was typically intermediate to those of the main stem. Protein percentage of top 'Hodgson 78' seeds was 1.1 and 1.5 percentage points lower in 1985 and 1986, respectively, than bottom seeds (Table 2). Top seeds contained more oil than seeds from bottom positions in 1986 (0.6 percentage points), but did not differ in 1985. The consistent nature of the differences in chemical composition across stem termination types suggests a common cause. In contrast, Collins and Cartter (1956) found that seeds from the bottom half of the main stem contained 0.5 percentage points more oil, and 1.0 percentage points less protein, than seeds from top positions. Environmental stress may have reduced seed mass and altered protein and oil content concurrently.

A SDD x AT x position interaction was linear for 'Hodgson 78' seed oil content in 1985 (Pr>F 0.01) and 1986 (Pr>F 0.10), but not for protein content (data not shown). Seeds from bottom positions of unstressed control plants that were exposed to an AT of 34 C both years contained 0.5 percentage points less oil than those from top positions, but bottom seeds from severely drought-stressed plants at 34 C contained 1.3 percentage points more oil than those from top positions. Therefore, chemical composition

differences due to position in our study were similar to those reported by Collins and Cartter (1956) if seeds from severely stressed plants at 34 C were considered.

Pod position during development affected the fatty acid composition of the total oil. 16:0 and 18:3 percentages in seeds from top positions of 'Gnome' and 'Hodgson 78' were lower than seeds from bottom positions (Table 3). 'Hodgson 78' seeds from top positions contained higher 18:1 and lower 18:2 percentages than seeds from bottom positions both years.

AT was stratified within the crop canopy; higher pod temperature was associated with top positions. On a whole-plant basis, stressfully-high ATs were associated with increased 16:0, 18:0, and 18:1, and decreased 18:2 and 18:3 (Paper 4, herein). These trends were consistent with changes in fatty acid composition in seeds from top positions. Similarly, changes in protein and oil content associated with seeds from top positions were consistent with changes in chemical composition because of high AT on a whole-plant basis. The data suggest that positional effects on protein and oil content, and fatty acid composition, may have been due to higher pod temperature associated with top positions.

Conclusions

Pod temperature did vary with AT, giving rise to increased pod temperatures at top positions. Pod temperature did not vary because of drought stress. Yield, seed number, and seed mass varied with position in a fashion dependent upon growth habit. The determinate cultivar produced larger seeds at top positions, whereas the indeterminate cultivar produced larger seeds at bottom positions. 'Gnome' seeds from top positions exhibited higher viability and vigor than bottom seeds, but 'Hodgson 78' seeds from bottom positions exhibited higher viability and vigor only in stressful environments. Reductions in viability and vigor were consistently associated with smaller seed mass. With both cultivars, seeds from top positions contained more oil, less protein, and less 18:2 and 18:3 than seeds from bottom positions. Seed mass, viability, and vigor differences associated with position were dependent upon growth habit, whereas compositional differences were dependent upon pod temperature. Selection using small seed samples and computer modelling efforts should consider the potential differences associated with position.

Table 1. Viability and vigor of soybean seeds that developed at three positions on determinate 'Gnome' and indeterminate 'Hodgson 78' plants

Position	Germination (%)		Seedling Axis Weight (mg seedling^{-1})		Conductivity (uMHOS g^{-1})		Hardseed (%)	
	1985	1986	1985	1986	1985	1986	1985	1986
'Gnome'								
Top	96.8	78.4	64.1	57.7	132	138	-	-
Bottom	92.8	73.0	60.4	55.3	146	148	-	-
Branch	98.0	73.2	62.7	52.6	165	168	-	-
SE	0.6	3.1	0.3	1.3	3	21	-	-
'Hodgson 78'								
Top	79.7	86.6	39.7	37.7	-	-	5.0	48.9
Bottom	79.7	86.1	39.5	37.9	-	-	5.6	29.9
SE	2.3	0.8	1.2	1.1	-	-	0.5	1.9

Table 2. Protein and oil content of soybean seeds that developed at three positions on determinate 'Gnome' and two positions on indeterminate 'Hodgson 78' plants

Position	Protein (%)		Oil (%)	
	1985	1986	1985	1986
		'Gnome'		
Top	41.3	39.5	20.4	22.2
Bottom	43.5	40.6	19.9	21.5
Branch	42.3	39.3	21.1	22.2
SE	0.1	0.4	0.2	0.2
		'Hodgson 78'		
Top	42.0	38.3	22.1	24.6
Bottom	43.1	39.7	21.7	24.0
SE	0.2	0.3	0.1	0.2

Table 3. Fatty acid composition of soybean seeds that developed at three positions on determinate 'Gnome' and two positions on indeterminate 'Hodgson 78' plants

Position	Palmitate (%)		Stearate (%)		Oleate (%)		Linoleate (%)		Linolenate (%)	
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
'Gnome'										
Top	10.0	10.9	2.7	3.9	34.8	19.7	44.3	57.8	8.2	7.8
Bottom	10.5	11.1	2.8	3.8	33.2	20.2	45.0	57.0	8.5	8.0
Branch	10.8	11.2	3.0	4.1	31.5	18.3	46.1	58.1	8.5	8.3
SE	0.1	0.1	0.1	0.0	0.9	0.2	0.7	0.2	0.1	0.1
'Hodgson 78'										
Top	11.9	11.2	4.0	3.7	26.4	28.5	51.3	50.8	6.5	5.8
Bottom	12.1	11.5	4.0	3.5	25.0	26.5	52.1	52.5	6.8	6.0
SE	0.1	0.1	0.1	0.0	0.3	0.1	0.2	0.1	0.1	0.1

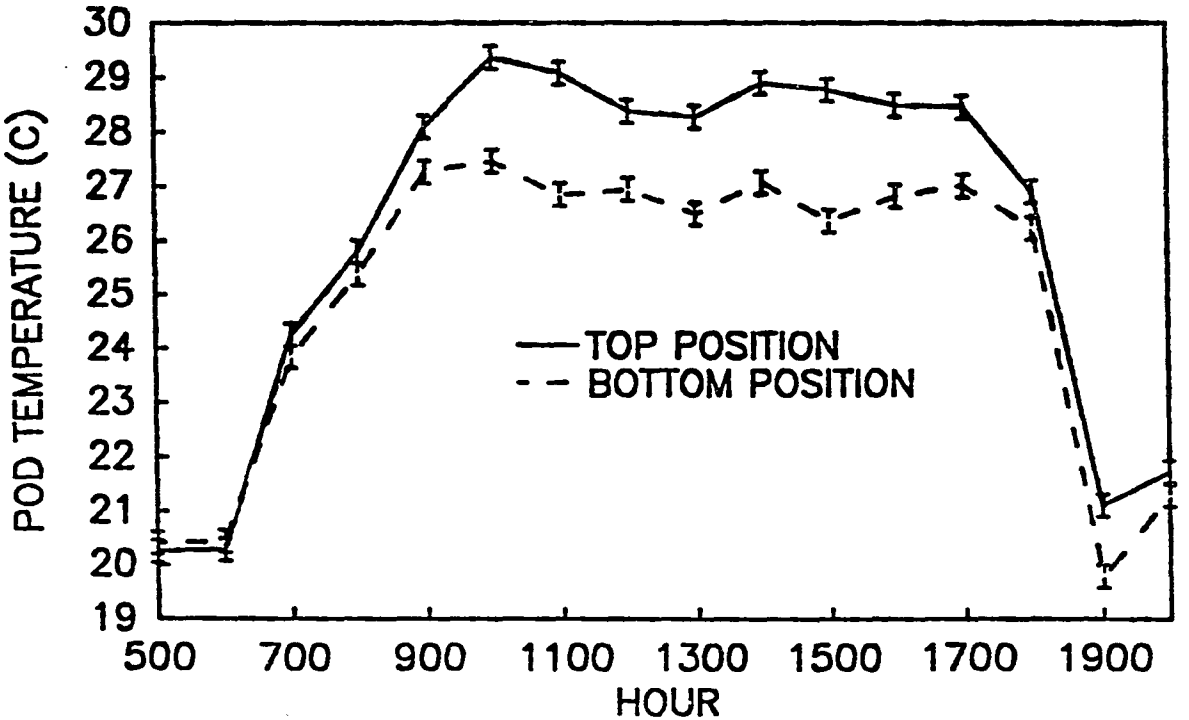


Figure 1. Diurnal variation in the temperature of pods from top and bottom positions of the soybean plant main stem

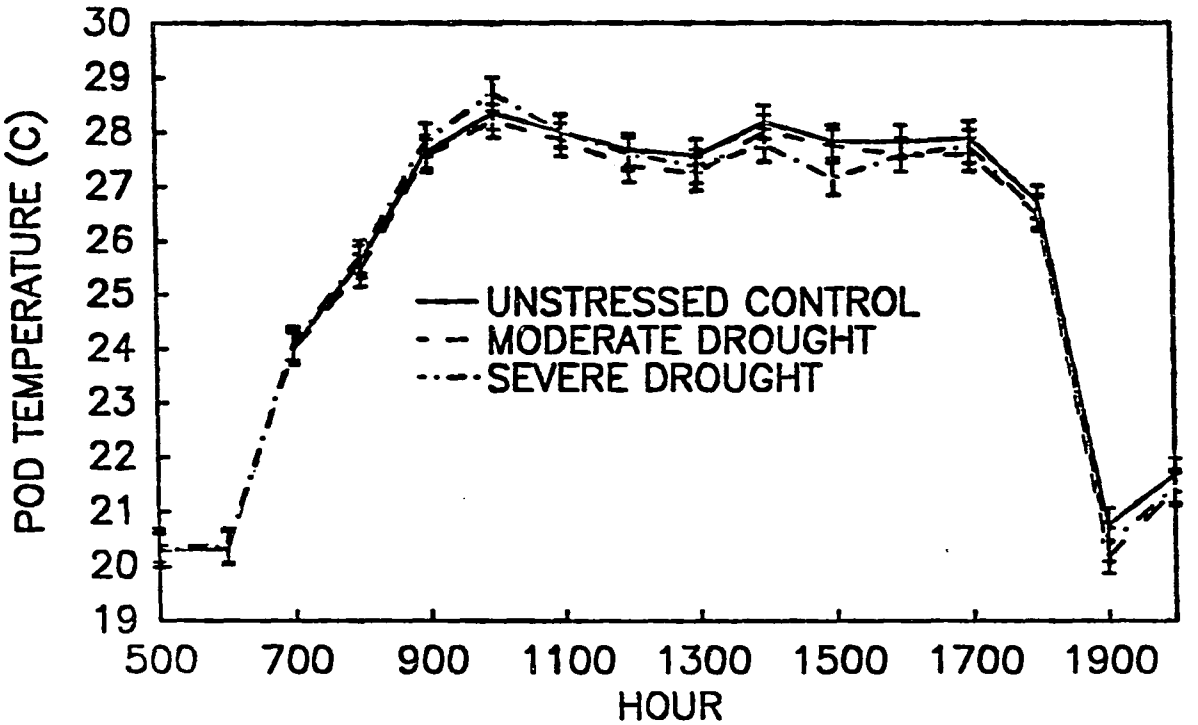


Figure 2. Diurnal variation in the temperature of pods from soybean plants exposed to three drought stress levels during seed fill

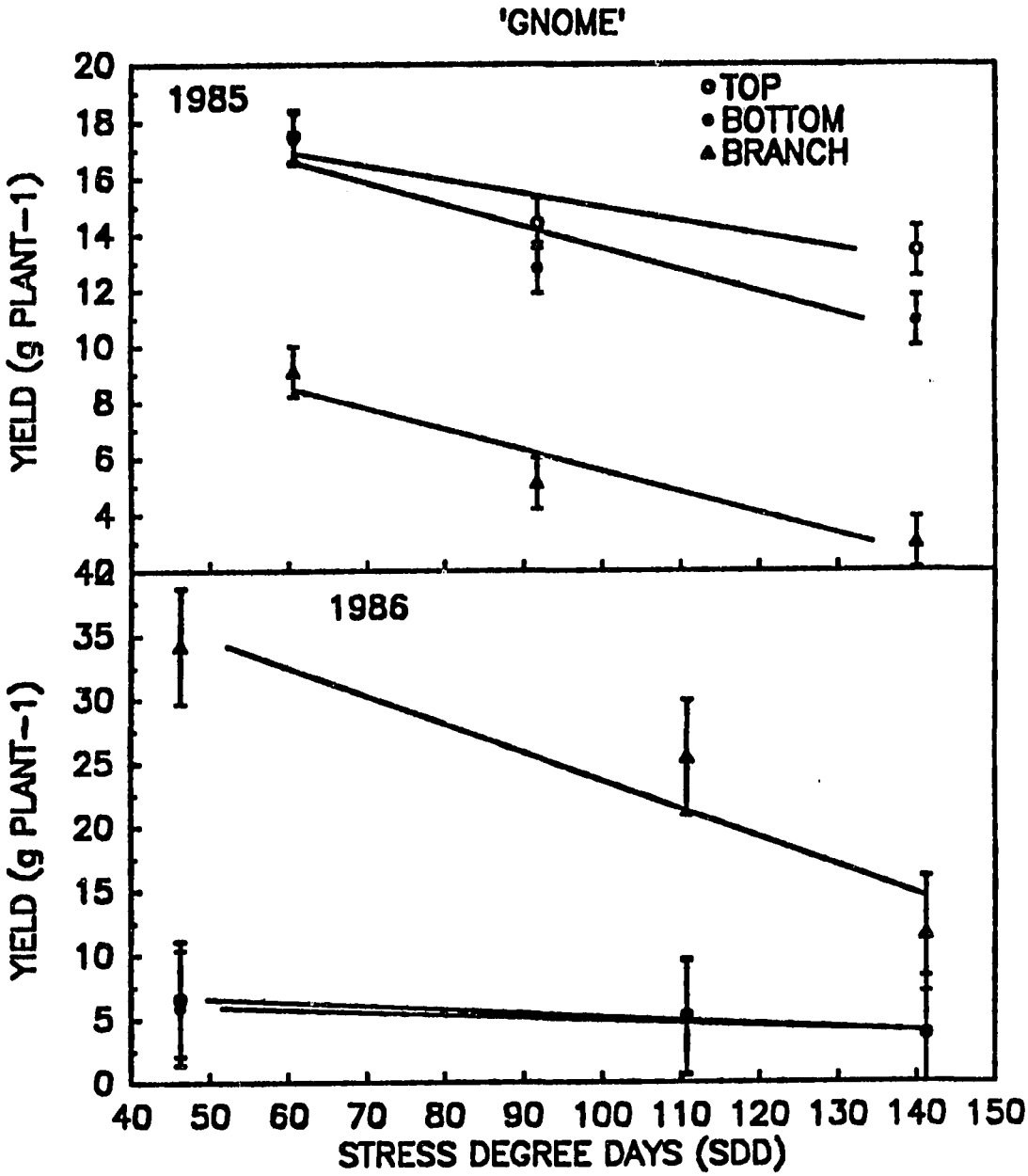
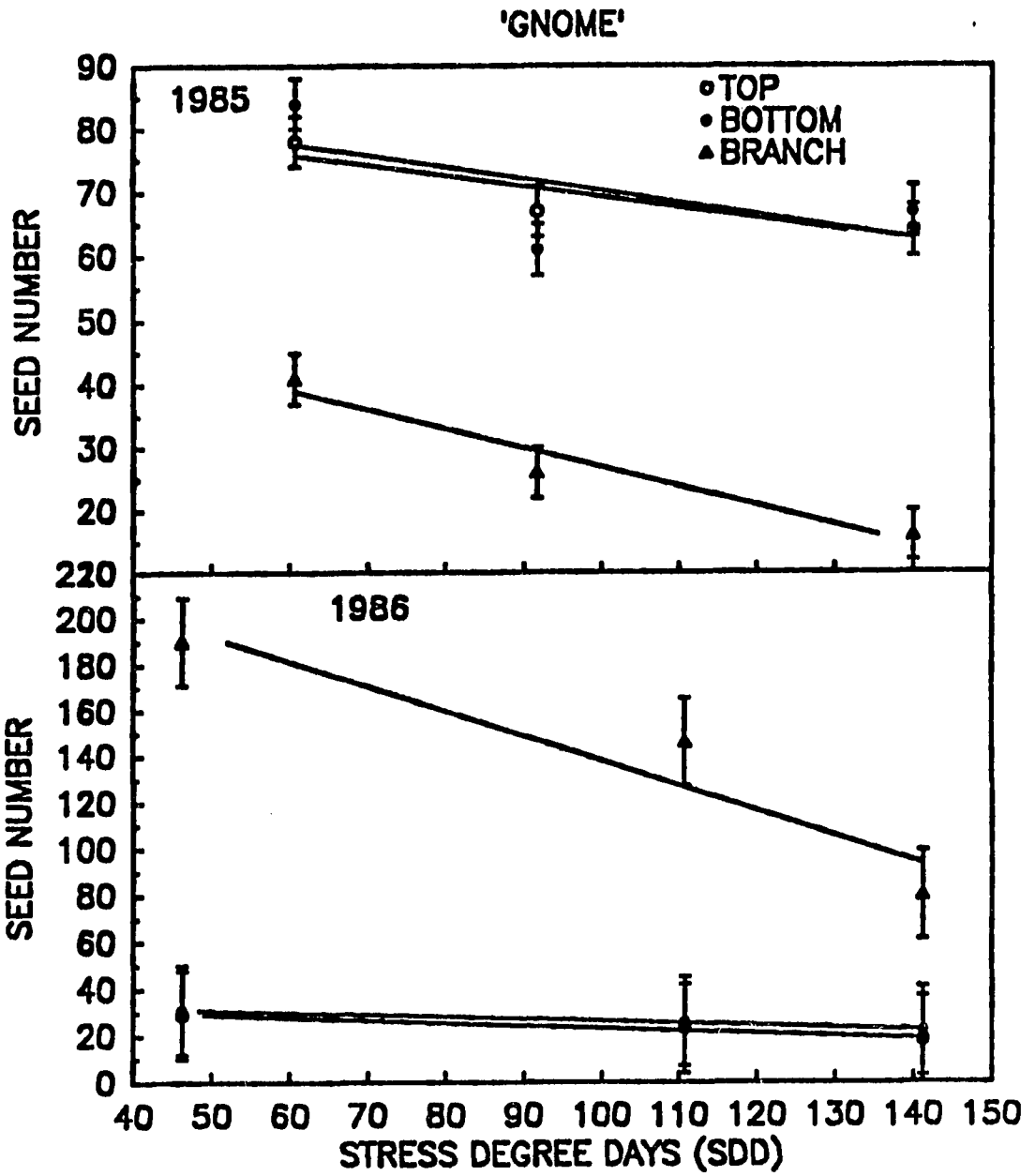
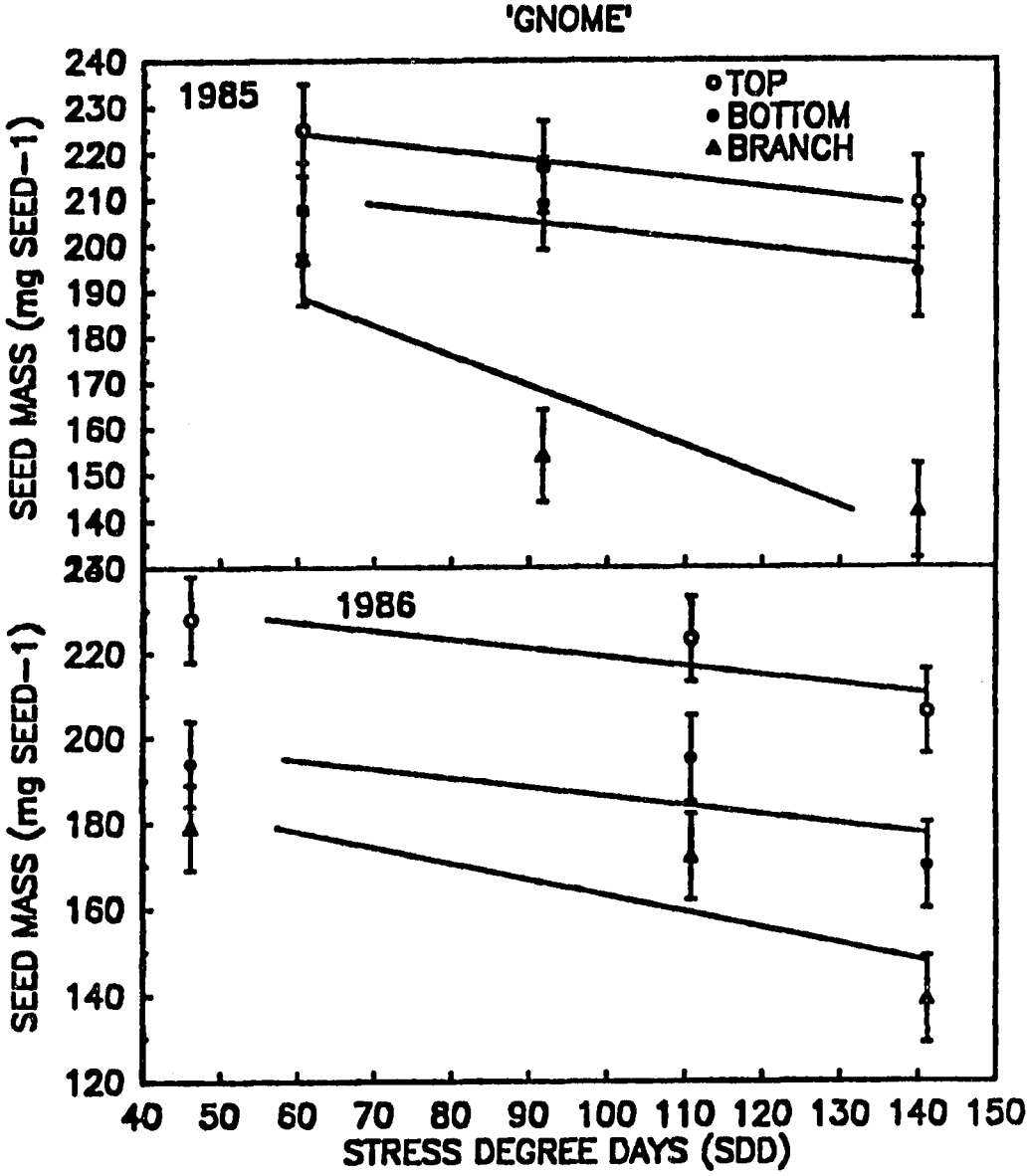


Figure 3. Reductions of 'Gnome' yield, seed number, and seed mass at top, bottom, and branch positions because of exposure to three drought stress levels during seed fill


'GNOME'
1985
TOP
BOTTOM
BRANCH
SEED NUMBER
1986
SEED NUMBER
STRESS DEGREE DAYS (SDD)


'GNOME'
1985
1986
TOP
BOTTOM
BRANCH
SEED MASS (mg SEED−1)
SEED MASS (mg SEED−1)
240
230
220
210
200
190
180
170
160
150
140
220
200
180
160
140
120
40 50 60 70 80 90 100 110 120 130 140 150
STRESS DEGREE DAYS (SDD)

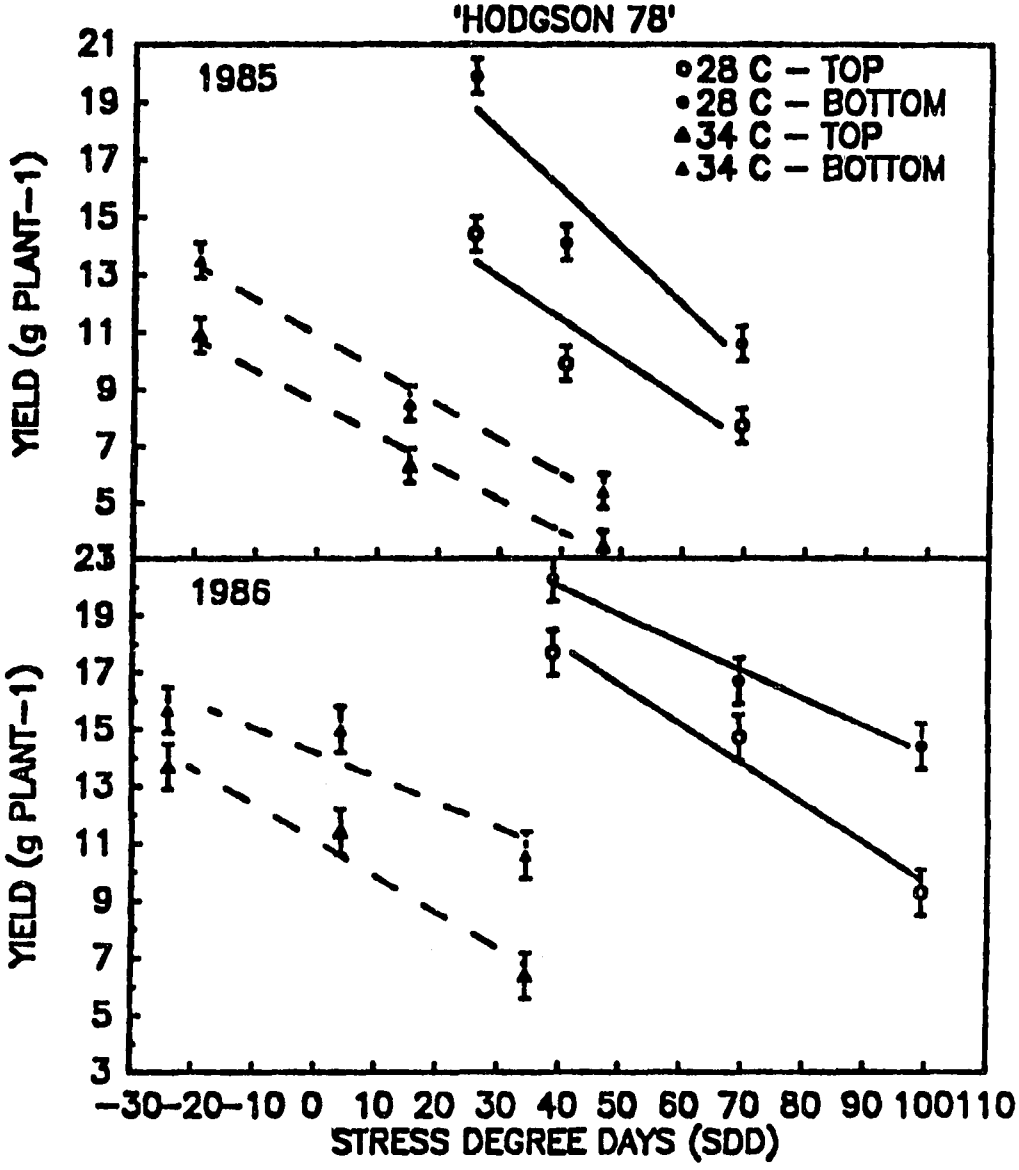
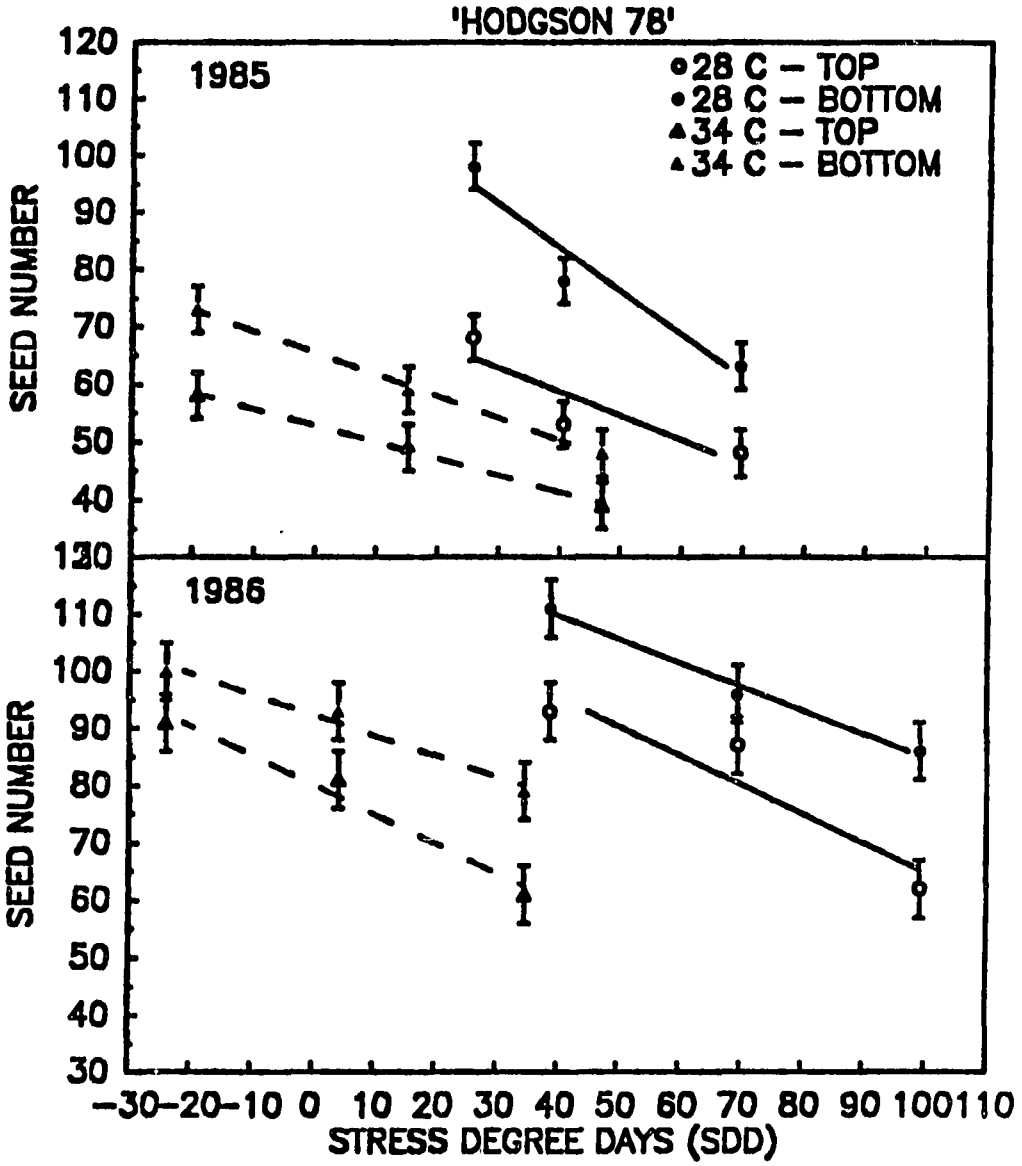
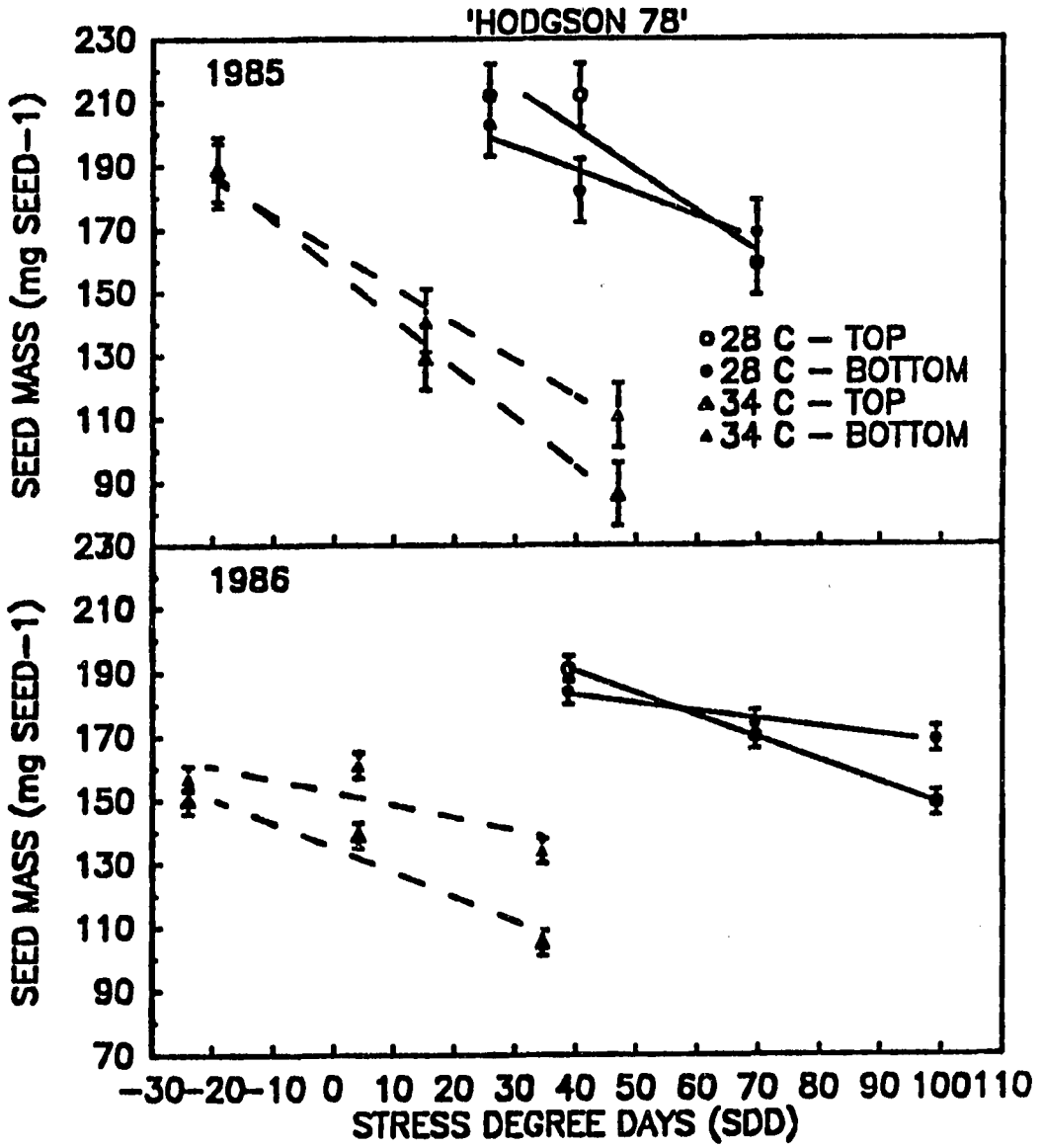


Figure 4. Reductions of 'Hodgson 78' yield, seed number, and seed mass at top and bottom positions because of three drought stress levels at an optimum and stressfully-high air temperature during seed fill


'HODGSON 78'
1985
1986
28 C – TOP
28 C – BOTTOM
34 C – TOP
34 C – BOTTOM
SEED NUMBER
SEED NUMBER
120
110
100
90
80
70
60
50
40
30
–30 –20 –10 0 10 20 30 40 50 60 70 80 90 100 110
STRESS DEGREE DAYS (SDD)


'HODGSON 78'
1985
1986
SEED MASS (mg SEED-1)
SEED MASS (mg SEED-1)
230
210
190
170
150
130
110
90
70
28 C — TOP
28 C — BOTTOM
34 C — TOP
34 C — BOTTOM
-30 -20 -10 0 10 20 30 40 50 60 70 80 90 100 110
STRESS DEGREE DAYS (SDD)

SUMMARY

Drought and high temperature (AT) stress occurred during soybean seed fill, reduced the seed yield, viability and vigor, and altered the chemical composition. The objective of this study was to impose and quantify drought stress at several ATs, then relate stress intensity to leaflet productivity, the yield components, seed viability and vigor, protein and oil content, and the fatty acid composition of the oil.

Control, moderate, and severe drought stresses were imposed on pot-grown soybean plants by applying differing volumes of water during seed fill at ATs of 20, 26, 27, 29, 33, and 35 C. Stress intensity was quantified by summing stress degree days (SDD), the average daily difference between leaf temperature (LT) and AT. SDD increased linearly as the water supply decreased and accurately indicated drought stress intensity within an AT treatment. LT predicted using energy budget relationships corresponded well with empirical data.

As SDD accumulated from 46.2 to 141.2 at 26 C, leaf resistance increased linearly by 2.2-fold and transpiration rate decreased linearly by 45%. Apparent photosynthetic rate decreased linearly from 0.85 to 0.26 mg CO_2 m^{-2} s^{-1}. These results suggest that SDD relate drought and reduced yield by detecting reduced photosynthetic rates. Yield was

reduced linearly 49% by drought and 29% by high AT. Severe drought at 34 C reduced the yield from 18.1 to 6.5 g seed plant^{-1}. Decreased seed number accounted for 80% of the yield loss. Individual seed mass was reduced by 20% by drought at 26 and 29 C, but by 47% at 35 C. Severe drought at the optimum AT caused fewer seeds to be produced, but severe drought at the stressfully-high AT caused both fewer and smaller seeds to be produced.

Standard germination and seedling axis dry weight of 'Gnome' seeds was reduced 6 and 9%, respectively, by severe drought at 20 and 26 C. Conductivity was increased by 17%. 'Hodgson 78' seed germination percentage was reduced 10% by severe drought, 3% by high AT, and 29% by a drought x AT interaction. Seed quality was correlated with single-seed mass (+0.89), when seed mass was reduced by stress. Reductions in seed viability and vigor by environmental stress were buffered by seed number. Seed viability and vigor were maintained when severe drought reduced yield and seed number, but when severe drought occurred at a stressfully-high AT, yield, seed number and mass, viability and vigor were reduced. The extent of viability and vigor loss was less than that of yield loss.

LT, predicted using energy budget relationships, compared well with empirically-measured LT. The utilization of a directly-measured plant parameter such as

LT that is responsive to the independent factors of the environment represents a potentially accurate method for quantifying stress. The ability to quantify stress intensity and the effects of stress on productivity and seed quality would facilitate the development of predictive computer models and irrigation management tools.

Environmental factors during seed fill affected the seed chemical composition, and therefore, utilization properties of the grain. Protein and oil content exhibited an inverse curvilinear relationship with AT. Maximum oil and minimum protein percent were 24.6 and 38.0, respectively, at 29 C. Severe drought reduced oil by 3% and increased protein by 5%. A SDD x AT interaction further reduced oil content and increased protein content. Linolenic and linoleic acid percentage decreased 19 and 5%, respectively, and oleic acid increased 13% at 34 C, suggesting the inhibition of oleic acid desaturase by high AT. Fatty acid composition was little affected by drought stress.

Pod temperature varied with AT giving rise to elevated pod temperatures at upper nodal positions. Yield, seed number, and seed mass varied with position because of differences in growth habit. Top seeds of determinate 'Gnome' exhibited greater seed mass, and higher viability and vigor than bottom seeds, but indeterminate 'Hodgson 78'

seeds from bottom positions exhibited larger mass and higher viability and vigor only in stressful environments. Regardless of growth habit, top seeds contained more oil, less protein, and less 18:2 and 18:3 than bottom seeds. These changes in composition with pod position were consistent with the changes associated with AT, suggesting that pod temperature may influence seed chemical composition. Because of the differences associated with position, care must be taken in selecting small seed samples for breeding studies and in computer modelling efforts of stress effects.

Membrane fluidity is determined by the composition of its constituent lipids in interaction with existing enviromental conditions. Membrane lipid composition is dynamically regulated in response to changes in AT to maintain optimum fluidity. Membranes that are not fluid leak cell solutes. The optimum lipid composition of a membrane that develops at a high AT differs from the optimum composition at a low AT. Seeds exposed to high AT during development leak a greater proportion of their solutes when imbibed at 25 C. Seeds that developed in the hot development environment exhibit poor membrane integrity, and reduced vigor, possibly because their constitutive membrane composition was not suitably adapted to the cooler imbibition environment.

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APPENDIX

'Gnome' Stress Intensity

Source of Variation	Degrees of Freedom	Stress Degree Days	Reproductive Period Duration
		1985	
Replication	2	63.91**	16.10
Drought	2	91.99**	246.08*
Linear	(1)	183.63*	401.77
Lack of Fit	(1)	2.35	90.39
Error	4	3.27	22.74
Linear	(2)		
Lack of Fit	(2)		
Total	8		
		1986	
Replication	2	15.05*	92.22
Drought	2	196.23**	1,045.16**
Linear	(1)	379.45**	2,043.08*
Lack of Fit	(1)	13.01	47.24
Error	4	1.58	26.25
Linear	(2)	0.07	72.19
Lack of Fit	(2)	3.09	19.69
Total	8		

*Significant at .05 level and applies to subsequent appendices.

**Significant at .01 level and applies to subsequent appendices.

'Gnome' Leaflet Productivity

Source of Variation	Degrees of Freedom	APs[1]	r_l[2]	E[3]
		1986		
Replication	2	0.59	24.2	35,662*
Drought	2	9.13**	73.9*	160,197**
Linear	(1)	17.96**	146.9**	315,163**
Lack of Fit	(1)	0.30	0.9	5,232
Error	4	0.19	4.7	4,186
Linear	(2)	0.08	1.0	2,818
Lack of Fit	(2)	0.30	8.4	5,554
Total	8			

[1]Apparent photosynthetic rate.

[2]Leaf resistance.

[3]Transpiration rate.

'Hodgson 78' Stress Intensity

Source of Variation	Degrees of Freedom	Stress Degree Days	Reproductive Period Duration
		1985	
Replication	2	5.6	38
Temperature	1	345.0**	1,476
Main Error	2	1.3	82
Drought	2	365.8**	1,503**
Linear	(1)	708.8**	3,003**
Lack of Fit	(1)	22.8*	3
Temperature x Drought	2	18.2**	191*
Linear	(1)	33.3**	376*
Lack of Fit	(1)	3.1	6
Subplot Error	8	0.6	25
Linear	(4)	0.3	20
Lack of Fit	(4)	0.9	30
Total	17		
		1986	
Replication	2	14.8	52*
Temperature	1	934.2**	469**
Main Error	2	2.9	2
Drought	2	257.1**	872**
Linear	(1)	507.7**	1,713**
Lack of Fit	(1)	6.4*	31
Temperature x Drought	2	0.1	23
Linear	(1)	0.2	1
Lack of Fit	(1)	0.1	44
Subplot Error	8	0.5	8
Linear	(4)	1.8	3
Lack of Fit	(4)	0.8	14
Total	17		

'Gnome' Yield and the Yield Components

Source of Variation	Degrees of Freedom	Yield	Pod Number	Seed Number
		1985		
Replication	2	1.7	27	22
Drought	2	73.6**	240*	932*
Linear	(1)	144.2**	473*	1,670*
Lack of Fit	(1)	3.0	8	193
Main Error	4	3.0	31	134
Linear	(2)	0.4	20	25
Lack of Fit	(2)	5.7	42	242
Position[1]	2	229.1**	796**	5,422**
T v. B	(1)	9.2**	57**	8
R v. T,B	(1)	448.9**	1,536**	10,836**
Drought x Position	4	1.2	10	65
Drought x T v. B	(2)	2.1	14	59
Drought x R v. T,B	(2)	0.3	6	70
Subplot Error	12	2.4	13	60
Drought x T v. B	(6)	0.6	3	16
Drougth x R v. T,B	(6)	4.2	22	104
Total	26			
		1986		
Replication	2	118.6	337	1,288
Drought	2	1,752.2**	6,211**	38,644**
Linear	(1)	3,118.7*	11,412**	70,018**
Lack of Fit	(1)	385.7*	1,010*	7,271**
Main Error	4	20.1	68	279
Linear	(2)	34.1	116	490
Lack of Fit	(2)	6.1	21	67
Position	2	10,999.2**	72,876**	403,091**
T v. B	(1)	4.0	140**	274
R v. T,B	(1)	21,994.5**	146,613**	805,908**
Drought x Position	4	949.0**	4,113**	23,398**
Drought x T v. B	(2)	2.2	1	18
Drought x R v. T,B	(2)	1,895.7**	8,225**	46,778**
Subplot Error	12	59.4	256	1,053
Drought x T v. B	(6)	3.6	6	53
Drought x R v. T,B	(6)	115.3	507	2,053
Total	26			

[1]T, B, and R represent top, bottom, and branch positions.

'Gnome' Yield and the Yield Components

Source of Variation	Degrees of Freedom	Seed Mass	Seed Number Per Pod
		1985	
Replication	2	3.5	0.083
Drought	2	18.7*	0.023
Linear	(1)	37.4*	0.011
Lack of Fit	(1)	0.0	0.035*
Main Error	4	1.4	0.020
Linear	(2)	1.0	0.040
Lack of Fit	(2)	1.9	0.001
Position	2	66.5**	0.538**
T v. B	(1)	8.0**	0.245**
R v. T,B	(1)	125.0**	0.831**
Drought x Position	4	5.4	0.133**
Drought x T v. B	(2)	0.4	0.122**
Drought x R v. T,B	(2)	10.4	0.104*
Subplot Error	12	2.7	0.008
Drought x T v. B	(6)	0.2	0.003
Drought x R v. T,B	(6)	5.3	0.013
Total	26		
		1986	
Replication	2	54.2	0.011
Drought	2	201.3*	0.260*
Linear	(1)	255.1*	0.444*
Lack of Fit	(1)	147.6	0.077
Main Error	4	12.1	0.029
Linear	(2)	2.7	0.015
Lack of Fit	(2)	21.6	0.043
Position	2	684.4**	1.037**
T v. B	(1)	465.3**	1.301**
R v. T,B	(1)	893.5**	0.773**
Drought x Position	4	8.2	0.168
Drought x T v. B	(2)	2.7	0.287
Drought x R v. T,B	(2)	13.6	0.049
Subplot Error	12	2.7	0.068
Drought x T v. B	(6)	3.4	0.090
Drought x R v. T,B	(6)	2.1	0.045
Total	26		

'Hodgson 78' Yield and the Yield Components

Source of Variation	Degrees of Freedom	Yield	Pod Number	Seed Number
		1985		
Replication	2	23.91	157.5	761.1
Temperature	1	1,644.15**	3,009.6**	13,875.0**
Main Error	2	8.19	17.3	55.4
Drought	2	1,540.20**	3,681.5**	14,453.1**
Linear	(1)	2,959.92**	7,251.5**	28,274.2**
Lack of Fit	(1)	120.48*	111.5	632.0
Drought x Temperature	2	0.86	61.4	258.8
Linear	(1)	0.44	107.0	334.8
Lack of Fit	(1)	1.27	15.7	182.8
Subplot Error	8	9.30	55.3	230.3
Linear	(4)	12.63	25.8	205.3
Lack of Fit	(4)	5.96	84.8	255.3
Position	1	755.94**	5,278.8**	21,823.1**
Temperature x Position	1	64.07**	306.3**	2,622.1**
Drought x Position	2	15.43*	171.8**	712.6**
Linear	(1)	30.59**	343.3**	1,423.9**
Lack of Fit	(1)	0.26	0.3	1.4
Temperature x Drought x Position	2	5.77	44.5*	189.9
Linear	(1)	11.43**	82.7*	336.4**
Lack of Fit	(1)	0.10	6.4	43.4
Sub-subplot Error	12	2.25	9.4	78.5
Linear	(6)	0.35	5.7	10.6
Lack of Fit	(6)	3.19	11.2	112.4
Total	35			

'Hodgson 78' Yield and the Yield Components

Source of Variation	Degrees of Freedom	Yield	Pod Number	Seed Number
		1986		
Replication	2	15.6	95.8	177.7*
Temperature	1	742.8**	242.7*	1,634.3**
Main Error	2	6.9	11.0	3.6
Drought	2	994.0**	2,628.7**	15,905.5**
Linear	(1)	1,937.8**	5,098.2**	30,936.1**
Lack of Fit	(1)	50.1	149.2	874.9
Drought x Temperature	2	16.5	18.4	43.6
Linear	(1)	7.3	31.1	63.7
Lack of Fit	(1)	25.7	5.7	23.4
Subplot Error	8	8.9	76.4	347.0
Linear	(4)	9.5	115.6	540.9
Lack of Fit	(4)	8.3	37.2	153.0
Position	1	726.1**	3,206.6**	15,399.9**
Temperature x Position	1	0.1	25.7	182.5
Drought x Position	2	35.1*	17.3	601.5*
Linear	(1)	65.7	21.5	615.9
Lack of Fit	(1)	4.5	13.0	587.2*
Temperature x Drought x Position	2	9.7	39.0	200.3
Linear	(1)	0.9	2.5	17.0
Lack of Fit	(1)	18.6**	75.5	383.6
Sub-subplot Error	12	4.0	25.5	154.0
Linear	(6)	9.5	45.2	334.4
Lack of Fit	(6)	1.3	15.6	63.8
Total	35			

'Hodgson 78' Yield and the Yield Components

Source of Variation	Degrees of Freedom	Seed Mass	Seed Number Per Pod
		1985	
Replication	2	4.6	0.022
Temperature	1	1,609.1*	0.018
Main Error	2	46.8	0.101
Drought	2	1,053.7**	0.153
Linear	(1)	2,098.1**	0.258
Lack of Fit	(1)	9.3	0.047
Drought x Temperature	2	139.9*	0.015
Linear	(1)	237.5**	0.016
Lack of Fit	(1)	42.4	0.004
Subplot Error	8	17.3	0.141
Linear	(4)	6.4	0.043
Lack of Fit	(4)	28.1	0.239
Position	1	5.6	0.250
Temperature x Position	1	57.9*	0.126
Drought x Position	2	39.5*	0.056
Linear	(1)	67.0*	0.003
Lack of Fit	(1)	12.0	0.108
Temperature x Drought x Position	2	8.8	0.034
Linear	(1)	1.8	0.009
Lack of Fit	(1)	15.7	0.058
Sub-subplot Error	12	6.6	0.101
Linear	(6)	5.4	0.067
Lack of Fit	(6)	7.1	0.118
Total	35		

'Hodgson 78' Yield and the Yield Components

Source of Variation	Degrees of Freedom	Seed Mass	Seed Number Per Pod
		1986	
Replication	2	11.2	0.126
Temperature	1	678.6*	0.021
Main Error	2	10.2	0.051
Drought	2	230.0**	0.078*
Linear	(1)	438.3**	0.149**
Lack of Fit	(1)	21.7	0.007
Drought x Temperature	2	16.9	0.066*
Linear	(1)	4.4	0.034*
Lack of Fit	(1)	29.5	0.098
Subplot Error	8	6.7	0.011
Linear	(4)	2.5	0.002
Lack of Fit	(4)	11.0	0.019
Position	1	118.7**	0.014
Temperature x Position	1	30.7**	0.004
Drought x Position	2	32.2**	0.190**
Linear	(1)	64.5**	0.189*
Lack of Fit	(1)	0.0	0.190**
Temperature x Drought x Position	2	0.6	0.004
Linear	(1)	0.4	0.003
Lack of Fit	(1)	0.8	0.004
Sub-subplot Error	12	1.0	0.013
Linear	(6)	1.9	0.013
Lack of Fit	(6)	0.5	0.013
Total	35		

'Gnome' Viability and Vigor

Source of Variation	Degrees of Freedom	Germ[1]	SADW[2]	Conductivity
		1985		
Replication	2	23.72	3.31	3.71**
Drought	2	51.72*	60.17	818.24
Linear	(1)	99.55*	119.56	1,501.95
Lack of Fit	(1)	3.89	0.77	134.52
Main Error	4	3.81	13.32	185.53
Linear	(2)	2.64	19.62	288.70
Lack of Fit	(2)	1.97	7.01	82.36
Position[3]	1	72.00**	58.68**	870.84*
Drought x Position	2	6.17	3.34	123.32
Linear	(1)	10.79	0.01	245.48
Lack of Fit	(1)	1.54	6.66*	1.17
Subplot Error	6	3.11	0.74	90.10
Linear	(3)	1.66	0.85	138.58
Lack of Fit	(3)	4.56	0.63	41.61
Total	17			
		1986		
Replication	2	18.80	12.97	1,952
Drought	2	346.81	117.01**	42,218
Linear	(1)	133.95	175.17**	65,169
Lack of Fit	(1)	559.67*	58.85	19,267
Main Error	4	382.31	4.35	6,234
Linear	(2)	738.53	1.65	5,504
Lack of Fit	(2)	26.09	7.06	6,964
Position[3]	2	84.68	59.59	26,815**
T v. B	(1)	130.68	27.13	-
R v. T,B	(1)	38.68	92.04	-
Drought x Position	4	151.30	6.58	7,430
Drought x T v. B	(2)	208.38	5.74	13,838
Drought x R v. T,B	(2)	94.23	7.42	1,023
Subplot Error	12	88.13	15.91	3,840
Drought x T v. B	(6)	72.93	13.57	5,218
Drought x R v. T,B	(6)	103.82	18.25	2,462

[1]Standard germination percentage.

[2]Seedling axis dry weight.

[3]T, B, and R represent top, bottom, and branch positions.

'Hodgson 78' Viability and Vigor

Source of Variation	Degrees of Freedom	Germination Percentage	SADW[1]
		1985	
Replication	2	750.6	295.3**
Temperature	1	14,214.1*	1,805.2**
Main Error	2	666.0	7.9
Drought	2	1,828.1*	424.4**
Linear	(1)	3,423.3	771.0**
Lack of Fit	(1)	232.8*	77.8
Drought x Temperature	2	1,438.5*	168.2**
Linear	(1)	2,841.2	302.9*
Lack of Fit	(1)	360.0	33.4
Subplot Error	8	278.4	17.9
Linear	(4)	532.8	16.9
Lack of Fit	(4)	24.1	18.9
Position	1	0.0	1.4
Temperature x Position	1	337.8	18.0
Drought x Position	2	415.0*	56.6
Linear	(1)	710.5	113.1*
Lack of Fit	(1)	119.5	0.2
Drought x Temperature x Position	2	293.1	123.4*
Linear	(1)	389.5	100.9**
Lack of Fit	(1)	196.6	146.9
Sub-subplot Error	12	92.4	25.8
Linear	(6)	107.0	1.8
Lack of Fit	(6)	85.0	37.8
Total	35		

[1]Seedling axis dry weight.

'Hodgson 78' Viability and Vigor

Source of Variation	Degrees of Freedom	Germination Percentage	SADW
		1986	
Replication	2	54.3	25.5*
Temperature	1	30.3	318.6**
Main Error	2	6.3	0.4
Drought	2	109.8**	86.2
Linear	(1)	197.5**	172.2*
Lack of Fit	(1)	22.0	0.3
Drought x Temperature	2	14.6	36.0
Linear	(1)	25.9*	13.9
Lack of Fit	(1)	3.3	58.2
Subplot Error	8	12.2	29.2
Linear	(4)	3.1	18.8
Lack of Fit	(4)	21.2	39.5
Position	1	10.0	0.3
Temperature x Position	1	20.3	8.7
Drought x Position	2	20.9	27.5
Linear	(1)	40.2	51.7
Lack of Fit	(1)	1.6	3.3
Drought x Temperature x Position	2	5.6	0.7
Linear	(1)	5.0	0.2
Lack of Fit	(1)	6.2	1.2
Sub-subplot Error	12	12.5	21.3
Linear	(6)	8.7	20.6
Lack of Fit	(6)	16.3	22.1
Total	35		

'Hodgson 78' Viability and Vigor

Source of Variation	Degrees of Freedom	Hardseed Percent	Conductivity
		1985	
Replication	2	1.2	1,455.5
Temperature	1	400.0*	342,439.5*
Main Error	2	3.1	3,539.8
Drought	2	30.6*	29,182.6
Linear	(1)	27.2	55,464.8
Lack of Fit	(1)	33.9*	2,900.3
Drought x Temperature	2	7.6	13,806.0
Linear	(1)	14.9	27,124.7
Lack of Fit	(1)	0.3	487.2
Subplot	8	4.2	7,499.2
Linear	(4)	6.5	10,783.5
Lack of Fit	(4)	1.9	4,215.0
Position	1	2.8	3,950.1
Temperature x Position	1	28.4*	999.6
Drought x Position	2	13.1	16,201.3
Linear	(1)	5.9	23,054.6
Lack of Fit	(1)	20.2	9,348.0
Temperature x Drought x Position	2	0.9	18,500.8
Linear	(1)	1.1	23,856.8
Lack of Fit	(1)	0.6	13,144.8
Sub-subplot Error	12	4.2	15,171.9
Linear	(6)	1.2	26,615.5
Lack of Fit	(6)	7.2	3,728.2
Total	35		

'Hodgson 78' Viability and Vigor

Source of Variation	Degrees of Freedom	Hardseed Percent	Conductivity
		1986	
Replication	2	535.5	4,378.5
Temperature	1	9,025.0*	2,472.6
Main Error	2	97.0	1,028.4
Drought	2	2,717.5**	492.0
Linear	(1)	5,173.6*	929.7
Lack of Fit	(1)	261.3	154.4
Drought x Temperature	2	424.3	607.4
Linear	(1)	564.4	1,208.5
Lack of Fit	(1)	284.3	6.4
Subplot Error	8	232.4	540.6
Linear	(4)	335.2	616.0
Lack of Fit	(4)	129.6	468.2
Position	1	3,249.0**	141.2
Temperature x Position	1	25.0	0.4
Drought x Position	2	206.3	342.5
Linear	(1)	168.8	49.7
Lack of Fit	(1)	243.9	635.3
Temperature x Drought x Position	2	499.0**	240.5
Linear	(1)	490.7*	216.0
Lack of Fit	(1)	507.4*	265.0
Sub-subplot Error	12	67.4	561.8
Linear	(6)	62.5	668.2
Lack of Fit	(6)	72.4	455.4
Total	35		

'Gnome' Protein and Oil Content

Source of Variation	Degrees of Freedom	Protein Percent	Oil Percent
		1985	
Replication	2	2.07*	0.09
Drought	2	37.27**	6.72*
Linear	(1)	73.77**	13.35*
Lack of Fit	(1)	0.76	0.10
Main Error	4	0.20	0.40
Linear	(2)	0.10	0.50
Lack of Fit	(2)	0.31	0.30
Position	1	22.45**	1.18
Drought x Position	2	3.02**	0.02
Linear	(1)	5.92*	0.04
Lack of Fit	(1)	0.12	0.01
Subplot Error	6	0.07	0.34
Linear	(3)	0.10	0.27
Lack of Fit	(3)	0.05	0.37
Total	17		
		1986	
Replication	2	5.46	2.83
Drought	2	56.42**	19.26**
Linear	(1)	103.55**	33.65*
Lack of Fit	(1)	9.28	4.87
Main Error	4	1.12	1.04
Linear	(2)	0.29	0.76
Lack of Fit	(2)	1.95	1.33
Position	1	4.33	1.47
Drought x Position	2	0.85	0.43
Subplot Error	6	1.77	0.34
Total	17		

'Hodgson 78' Protein and Oil Content

Source of Variation	Degrees of Freedom	Protein Percent	Oil Percent
		1985	
Replication	2	1.1	0.7
Temperature	1	147.6**	59.0*
Main Error	2	1.2	1.2
Drought	2	84.4**	53.6**
Linear	(1)	168.0**	107.0**
Lack of Fit	(1)	0.7	0.2
Temperature x Drought	2	9.0**	9.0**
Linear	(1)	0.2	17.6**
Lack of Fit	(1)	17.7*	0.4
Subplot	8	0.7	0.4
Linear	(4)	0.1	0.1
Lack of Fit	(4)	1.3	0.7
Position	1	10.8**	0.9
Temperature x Position	1	0.8	1.4*
Drought x Position	2	1.3	0.1
Linear	(1)	2.7	0.2
Lack of Fit	(1)	0.0	0.0
Temperature x Drought x Position	2	1.0	3.5**
Linear	(1)	1.5	6.3**
Lack of Fit	(1)	0.6	0.7
Sub-subplot Error	12	1.0	0.3
Linear	(6)	1.6	0.2
Lack of Fit	(6)	0.7	0.4
Total	35		

'Hodgson 78' Protein and Oil Content

Source of Variation	Degrees of Freedom	Protein Percent	Oil Percent
		1986	
Replication	2	0.9	0.7
Temperature	1	37.2*	1.8*
Main Error	2	1.9	0.1
Drought	2	29.7**	13.8**
Linear	(1)	56.3**	24.9**
Lack of Fit	(1)	3.1	2.7
Temperature x Drought	2	3.7	2.0
Linear	(1)	6.7	3.7
Lack of Fit	(1)	0.7	0.4
Subplot Error	8	1.3	1.1
Linear	(4)	1.0	0.7
Lack of Fit	(4)	1.5	1.4
Position	1	19.1*	3.1*
Temperature x Position	1	2.9	0.5
Drought x Position	2	1.3	1.0
Linear	(1)	0.1	0.2
Lack of Fit	(1)	2.6	1.7
Temperature x Drought x Position	2	0.8	2.0
Linear	(1)	1.4	0.9
Lack of Fit	(1)	0.3	3.2
Sub-subplot Error	12	2.1	0.5
Linear	(6)	2.6	0.4
Lack of Fit	(6)	1.5	0.6

'Gnome' Fatty Acid Composition

Source of Variation	Degrees of Freedom	16:0 %	18:0 %	18:1 %
		1985		
Replication	2	0.087	0.062	21.35*
Drought	2	0.295*	0.061	21.64*
Linear	(1)	0.520*	0.045	36.52*
Lack of Fit	(1)	0.069	0.077	6.76
Main Error	4	0.038	0.016	2.37
Linear	(2)	0.027	0.008	0.64
Lack of Fit	(2)	0.048	0.025	4.09
Position	2	1.487**	0.287**	23.54
T v. B	(1)	1.013**	0.058	11.60
R v. T,B	(1)	1.961**	0.516**	35.48
Drought x Position	4	0.095	0.046	4.83
Drought x T v. B	(2)	0.009	0.017	0.60
Drought x R v. T,B	(2)	0.181	0.076	9.07
Subplot Error	12	0.064	0.024	6.52
Drought x T v. B	(6)	0.036	0.019	6.35
Drought x R v. T,B	(6)	0.092	0.028	6.70
Total	26			
		1986		
Replication	2	0.033	0.032	1.72
Drought	2	0.925**	0.145	10.10
Linear	(1)	1.681*	0.023	13.86**
Lack of Fit	(1)	0.169	0.267	6.33
Main Error	4	0.028	0.176	1.55
Linear	(2)	0.040	0.038	0.12
Lack of Fit	(2)	0.016	0.314	2.98
Position	2	0.228**	0.287**	8.93**
Drought x Position	4	0.029	0.033	0.92
Subplot Error	12	0.019	0.007	0.53
Total	26			

'Gnome' Fatty Acid Composition

Source of Variation	Degrees of Freedom	18:2 %	18:3 %
	---------- 1985 ----------		
Replication	2	14.08*	0.855*
Drought	2	17.29*	0.004
Linear	(1)	32.73*	0.000
Lack of Fit	(1)	1.85	0.007
Main Error	4	1.19	0.094
Linear	(2)	0.38	0.062
Lack of Fit	(2)	2.01	0.126
Position	2	7.70	0.278
T v. B	(1)	2.07	0.520*
R v. T,B	(1)	13.33	0.035
Drought x Position	4	3.18	0.064
Drought x T v. B	(2)	0.91	0.058
Drought x R v. T,B	(2)	5.45	0.069
Subplot Error	12	4.12	0.107
Drought x T v. B	(6)	0.63	0.070
Drought x R v. T,B	(6)	4.28	0.143
Total	26		
	---------- 1986 ----------		
Replication	2	2.87*	0.272
Drought	2	5.73**	2.792*
Linear	(1)	10.20*	3.895**
Lack of Fit	(1)	1.27	1.689
Main Error	4	0.49	0.179
Linear	(2)	0.18	0.027
Lack of Fit	(2)	0.81	0.331
Position	2	2.99*	0.602*
Drought x Position	4	0.26	0.507**
Subplot Error	12	0.46	0.089
Total	26		

'Hodgson 78' Fatty Acid Composition

Source of Variation	Degrees of Freedom	16:0 %	18:0 %	18:1 %
		1985		
Replication	2	0.11	0.04	2.0
Temperature	1	0.03	8.81**	168.9**
Main Error	2	0.13	0.04	0.6
Drought	2	0.15	0.12*	1.8
Linear	(1)	0.26	0.11	2.2
Lack of Fit	(1)	0.04	0.12	1.5
Temperature x Drought	2	0.15	0.07	6.2*
Linear	(1)	0.25	0.14	11.6*
Lack of Fit	(1)	0.05	0.01	0.7
Subplot Error	8	0.11	0.02	1.2
Linear	(4)	0.07	0.03	1.3
Lack of Fit	(4)	0.15	0.02	1.1
Position	1	0.36*	0.03	16.2*
Temperature x Position	1	0.06	0.00	0.0
Drought x Position	2	0.23	0.13	8.8*
Linear	(1)	0.35	0.24	17.3*
Lack of Fit	(1)	0.11	0.03	0.3
Temperature x Drought x Position	2	0.10	0.03	1.2
Linear	(1)	0.20	0.05	2.1
Lack of Fit	(1)	0.00	0.01	0.3
Sub-subplot Error	12	0.07	0.08	1.1
Linear	(6)	0.12	0.08	1.0
Lack of Fit	(6)	0.05	0.09	1.1
Total	35			

'Hodgson 78' Fatty Acid Composition

Source of Variation	Degrees of Freedom	16:0 %	18:0 %	18:1 %
		1986		
Replication	2	0.17	0.17	2.9
Temperature	1	2.57	0.66	81.5*
Main Error	2	0.38	0.06	1.4
Drought	2	0.12	0.02	8.1
Linear	(1)	0.17	0.01	16.2
Lack of Fit	(1)	0.07	0.03	0.1
Temperature x Drought	2	0.02	0.07*	0.6
Linear	(1)	0.01	0.12*	1.0
Lack of Fit	(1)	0.04	0.02	0.1
Subplot Error	8	0.04	0.01	2.3
Linear	(4)	0.03	0.01	4.0
Lack of Fit	(4)	0.06	0.01	0.7
Position	1	0.43*	0.17**	36.6**
Temperature x Position	1	0.03	0.00	0.5
Drought x Position	2	0.00	0.05*	4.1**
Linear	(1)	0.01	0.04*	5.9**
Lack of Fit	(1)	0.00	0.05	2.3*
Temperature x Drought x Position	2	0.00	0.00	1.8**
Linear	(1)	0.00	0.00	1.0
Lack of Fit	(1)	0.00	0.00	2.6*
Sub-subplot Error	12	0.05	0.01	0.2
Linear	(6)	0.02	0.01	0.2
Lack of Fit	(6)	0.08	0.02	0.3
Total	35			

'Hodgson 78' Fatty Acid Composition

Source of Variation	Degress of Freedom	18:2 %	18:3 %
	1985		
Replication	2	0.8	0.18
Temperature	1	135.1**	17.29*
Main Error	2	0.3	0.07
Drought	2	3.6	0.30
Linear	(1)	7.3	0.16
Lack of Fit	(1)	0.0	0.44
Temperature x Drought	2	8.6**	0.04
Linear	(1)	16.4*	0.05
Lack of Fit	(1)	0.7	0.02
Subplot Error	8	0.8	0.11
Linear	(4)	1.0	0.15
Lack of Fit	(4)	0.7	0.06
Position	1	6.3**	1.13**
Temperature x Position	1	0.1	0.09
Drought x Position	2	9.7**	0.09
Linear	(1)	18.9**	0.09
Lack of Fit	(1)	0.4	0.10
Temperature x Drought x Position	2	0.7	0.36
Linear	(1)	0.7	0.69
Sub-subplot Error	12	0.6	0.11
Linear	(6)	0.5	0.23
Lack of Fit	(6)	0.7	0.05
Total	35		

'Hodgson 78' Fatty Acid Composition

Source of Variation	Degrees of Freedom	18:2 %	18:3 %
		1985	
Replication	2	0.4	0.57
Temperature	1	19.5	14.58**
Main Error	2	3.1	0.11
Drought	2	7.0*	0.11
Linear	(1)	13.5	0.00
Lack of Fit	(1)	0.5	0.22
Temperature x Drought	2	0.1	0.03
Linear	(1)	0.2	0.06
Lack of Fit	(1)	0.0	0.00
Subplot Error	8	1.4	0.17
Linear	(4)	2.2	0.31
Lack of Fit	(4)	0.6	0.03
Position	1	27.2**	0.33
Temperature x Position	1	0.0	0.11
Drought x Position	2	3.1**	0.08
Linear	(1)	5.4**	0.00
Lack of Fit	(1)	0.8	0.17
Temperature x Drought x Position	2	1.8**	0.05
Linear	(1)	1.5**	0.06
Lack of Fit	(1)	2.0*	0.03
Sub-subplot Error	12	0.2	0.07
Linear	(6)	0.1	0.01
Lack of Fit	(6)	0.2	0.14
Total	35		